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XANTHOPHORES IN FUNDULUS, WITH SPECIAL CONSIDERATION OF THEIR "EXPANDED" AND "CONTRACTED" PHASES

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The actual form of the dermal xanthophore in its so-called "expanded" and "contracted" states[1] is but loosely and imperfectly understood. So far as I have been able to discover, there are no adequate descriptions regarding it. Existing accounts are at best fragmentary, and hence, inconclusive. This lack is explained in part by the fact that there is still considerable doubt as to what really constitutes the xanthophore. It is partly accounted for also on the ground that this small[2] yellow cell rarely appears clearly visible under the microscope, its peripheral outline usually remaining vague, hazy and indefinite. Moreover, permanent histological preparations are practically valueless for a study of structures such as this. The carotinoid pigments and other lipochromes are readily dissolved in the alcohols and other organic solvents used in the course of tissue preparation, so that ultimately the yellow cells become quite indistinguishable from others. It has been necessary, therefore, to make observations in the main on living materials. This latter method of approach has many limitations, and has yielded for us but a partial knowledge of the true nature of the xanthophore.

As to just what moves when a xanthophore reacts is still an unsettled question. Many hypotheses have been forthcoming, but of these only the two main ones have the support of the majority of investigators in this field. One group describes the xanthophore as an ameboid cell, which extends and retracts its pigment-filled processes through the intercellular spaces of the surrounding tissues. The other group believes that there is, in a more or less fluid cytoplasm, an intracellular migration of the pigment into fixed processes and out of them, the cell outline remaining relatively unchanged. Each of these hypotheses has its weaknesses in the light of existing evidences. Ameboid movement has been observed frequently in

the melanophores of larval fishes, but its occurrence in the color cells of adults yet remains undemonstrated. Moreover, it is difficult to reconcile with those recorded observations of independent, random movements of the color granules or droplets throughout the cytoplasm, the idea of purely ameboid distribution of the pigment. The other hypothesis, which is the one more generally and more recently accepted, lacks the confirmation for the fixed cell outlines. The diffuse, tenuous condition of the cell processes, which are usually much obscured by overlying and adjoining cells, eludes differentiation by the microscope, and renders detection of their peripheral boundaries very difficult.

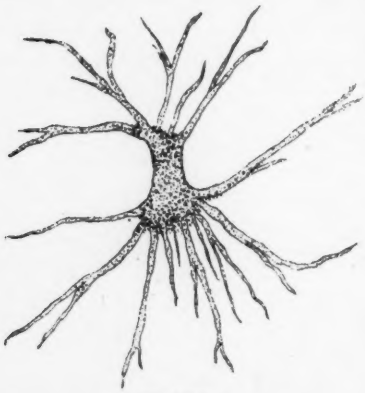

FIGURE 1

Camera lucida drawing (Leitz microscope, Oc. 10 ×, Obj. 4 mm.) Magn. × 640.

Normal maximally expanded xanthophore, showing outline of the delicate cell processes. The carotinoid pigment, which is represented by the fine stippling, has uniform distribution throughout the cell. Orange-red granules, indicated by the black dots, are unequally dispersed throughout the cytoplasm of the cell body and processes. No specific stain was employed, hence the nucleus cannot be indicated here. This cell was of uniform sulphur-yellow color.

The xanthopores of adult fishes have been described by many workers (Ballowitz, '13, '16; Kuntz, '17; Fries, '31; and also in the recent review by Biedermann, '26), hence a detailed account of their structure here becomes unnecessary. The purpose of this investigation was to determine the form actually assumed by the expanded, expanding or contracting, and contracted xanthophores, without special attention to cytological detail.

During the past months I examined isolated scales which I had removed from the trunk and tail regions of Fundulus heteroclitus L. I was able to obtain many which had become partly freed through a parasitic infection. When these were mounted on glass slides in a few drops of Ringer's solution, many cells became detached and floated freely in the medium. Among them were xanthophores in various states of expansion and contraction. All revealed distinct cell outlines, though few of them possessed extended processes. In many, a halo of clear, apparently homogeneous cytoplasm surrounded a more or less diffused, or a compacted pigment body. Vital staining with brilliant cresyl blue made still more evident the contrast between the cytoplasmic regions, the yellow center or xanthom (Ballowitz) and the clear nucleoplasm. The appear-

ances of these degenerating yellow cells suggested the probable form of the normal cells in their ordinary environment.

Fortunately, I was enabled to employ a technique which facilitated observation on normal freshly fixed material. From fishes which had become adapted to yellow and to black backgrounds I removed small thin scales, and put them directly into Stockard's solution. In this fluid a rapid fixation took place, and a beautiful clearing of the tissues occurred within a few hours. Clearing was further perfected when single scales were mounted on glass slides in a few drops of Brunn's glucose medium (generally used for the clearing of frozen sections). For the specific staining of the nuclei, a dilute solution of acetic methyl green was added to the fixing

FIGURE 2

Camera lucida drawing (Leitz microscope, Oc. 10 ×, Obj. 4 mm.) Magn. × 640. Two normal xanthophores in states of partial contraction or expansion, showing definite outlines. Both cells had been stained with methyl green, so that there appears distinctly in (*a*) one oval nucleus, and in (*b*) two nuclei, one of which is oval, the other somewhat rounded. The yellow carotinoid, which is represented by fine stippling, is unequally distributed, much of it being concentrated in the cell body. The orange-red granules, indicated by black dots, are unevenly dispersed in the cell body and in the processes. The central region of the cell was of yellowish orange color. Peripheral areas were faint yellow.

fluid. Very satisfactory results were obtained if the dye was allowed to diffuse into the lipochrome cells for a day or longer. This treatment of individual scales rendered the outlines of the delicate cell processes plainly visible, and displayed more thoroughly within them the protoplasmic arrangement that could not readily be detected in the living cells. The sulphur-yellow and orange-yellow carotinoids were always to be found included *within* the cytoplasm itself, though their marginal limits, save in maximal contraction, were generally diffuse and indistinct. There also occurred, though in irregular distribution throughout the pigment mass and the cytoplasm, many rather prominent brownish red or orange-red granule-like bodies. These were found frequently in isolated positions in the processes of expanded and contracted cells. The fact that some orange-

red granules were not always drawn toward the central body during the compacting movements of the pigment, but remained remotely distributed in the processes, was clear indication to me that the cytoplasm was constantly present within them. This inference was substantiated further by the appearance at times of oval or rounded nuclei in locations remote from the center of the cell. One or even two of them not infrequently were observed out in the larger cell processes.

The accompanying three figures, which are camera lucida drawings of xanthophores observed under the high power of the microscope, illustrate how the lipochromes are distributed in cells with maximal expansion, partial expansion or contraction, and maximal contraction of these pigments. The outline of each cell is definite, and, as specific staining reveals, the nuclear boundaries are also. Figure 1 represents a xanthophore at maximal expansion. Figure 2 shows two such cells in stages of pigment distribution intermediate between full expansion and full contraction. Each of these cells had been stained previously with acetic methyl green; one of them demonstrates a single nucleus, while the other indicates the presence of two. Figure 3 is that of a yellow cell with maximal pigment contraction. This one shows that the colored material is not entirely included within the small compacted central body, for, when this cell was examined under much restricted illumination, there was a faint glimmer of yellow in the cytoplasm. In each figure the carotinoid pigments are represented by means of fine dots, and the orange-red or brown-red granule-like bodies by the heavier black ones. The intensity of color in the distribution of these pigments is indicated by the frequency and the amount of stippling. In general, fully expanded cells are sulphur-yellow, partly expanded or contracted cells are shaded with orange and fully contracted cells are deep orange-yellow or orange. Only cells which

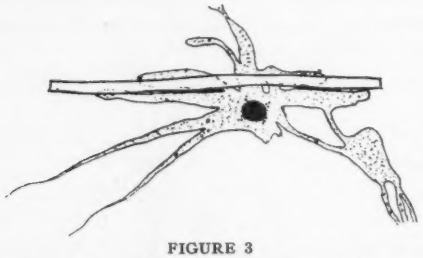

FIGURE 3

Camera lucida drawing (Leitz microscope. Oc. 10 ×, Obj. 4 mm.) Magn. × 400.

Normal maximally contracted xanthophore, showing distinct peripheral outline. Cell partly hidden by small overlying blood vessel. Carotinoid pigment, represented by stippling, is mostly aggregated in a compact deeply orange-colored central mass. There is, however, a very faint glimmer of yellow throughout the cytoplasm of the cell body and of the processes. Orange-red granules, indicated by black dots, are clustered near the pigment "ball," though some are distributed in certain cell processes. No nucleus is here represented. The compacted pigment mass was of deep orange-yellow or orange color. The cytoplasmic portions usually are invisible, because of almost complete absence of color.

apparently lack the orange-red granules have sulphur-yellow color in their contracted states.

The foregoing observations are very similar to those made by Franz ('08) on larvae of Pleuronectes platessa. This writer found in one particular case the unmistakably clear outlines of yellow cells, the pigments of which had been withdrawn from their processes. The recent work of Becher ('29), on hatching Coregonus fera, also reveals that the yellow pigment is but a portion of the xanthophore cell. Kuntz ('16) observed in larval Lucania parva that pigment movement did take place independently of the ameboid activity of the developing cell. I am not aware that such complete observations have been made on the fully-formed cells in the post-larval stages of fishes. Ballowitz ('13, '16) has seen, in Gobius and in Blennius, radial migrations of pigment granules in the cytoplasm, toward the central body (xanthom) and away from it. Kuntz ('17) has noted that pigment granules move in less regular arrangement in the cytoplasm of the xanthophores of Paralichthys albiguttus. Neither of these authors, however, has seen definite cell outlines in other than those of the expanded cells. (Ballowitz ('13) has illustrated by a beautiful set of figures what he claims to have observed for the erythrophores of Mullus L. The tiny red granules were seen passing through the cytoplasm in radial processions by a temporarily stationary nucleus. He was not able, however, to distinguish the peripheral limits of these minute red cells.) Fries ('31) often failed to discern any structural differentiation of the yellow cells in Fundulus, and thought that the diffuse coloration of the xanthophore represented a solution of the pigment in the continuous phase of the colloidal cell contents. Ballowitz ('13) had previously admitted the possibility of some yellow substance existing in solution in the cytoplasm, but he regarded this as of relative unimportance. My own observations on living cells in Fundulus have revealed that the pigment does exist in two states: one in which the color is diffused in a homogeneous manner through the cytoplasm; the other in which it has a distinct granular or droplet-like appearance. The former condition usually obtains in the expanded phases of the cell, the latter during the contracted states, when it is often indicated by the rapid motion, resembling Brownian movement, of the yellow particles.

According to the views of Spaeth ('16), the melanophore is a physicochemical system in which a colloidal suspension of melanin granules (the disperse phase) exists in a dispersion medium, which is an exceedingly fluid sort of protoplasm (the continuous phase), i.e., an emulsoid gel. To him, therefore, contraction and expansion in melanophores are similar to gelation and solation of emulsoids. This opinion has received much support from recent observers of the melanophore. The observations of Fries ('31), as well as those of myself, with reference to the dispersion of the

yellow pigment substances, make it appear that this physico-chemical condition is true also for the xanthophore. This interpretation is in harmony with the observations I have made on both the living and the fixed materials, and serves to explain, in part at least, the apparently stationary condition of the xanthopore in its varied phases of expansion and contraction.

The solution to the problem of the actual form of expanded and contacted melanophores, in adult fishes, has not escaped detection by observers for so long a time. The experiments of Spaeth ('14) and others, by whom photographs were made successively of individual expanded melanophores, later contracted, then re-expanded, have shown that the same processes were present after each expansion of these cells. The recent work of Matthews ('31), by whom tissue culture methods and microdissection technique were employed, has established beyond reasonable doubt that the processes of melanophores are of relatively fixed and constant form.

Although experimental methods have not yet been successfully employed to reveal the actual form of the xanthophore, the behavior of its cell contents, as recorded by many observers, implies that changes in the distribution of its pigment take place in essentially the same manner as they do in the malanophore. Moreover, my observation of its distinct outline strongly suggests that the form of the xanthophore, in its expanded and contracted phases, is a constant one.

This investigation was undertaken at the suggestion of Professor G. H. Parker, whose helpful counsel and supervision I am happy to acknowledge. I am indebted also to Dr. A. B. Dawson, whose suggestions in cytological technique have been invaluable in this work.

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[1] The use of the terms "expansion" and "contraction" in this paper is solely one of convenience, and for the sake of simplicity. It is not intended that they should be construed to imply an ameboid movement of the cell processes.

[2] In Fundulus, 9 to 50 microns in diameter; average diameter 25 microns.

EXPERIMENTS IN BIRD MIGRATION

III. The Effects of Artificial Light, Castration and Certain Extracts on the Autumn Movements of the American Crow (Corvus brachyrhynchos)

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Communicated September 24, 1932

The experiments of which this paper gives an account are a continuation of those previously described.[1,2,3] The present undertaking was made possible through grants from the U. S. National Research Council, the Elizabeth Thompson Fund and the Government Grant Committee of the Royal Society, London. The writer is also greatly indebted to Mr. H. B. Conover, who gave him further assistance. In addition he wishes to express his thanks to Professors Earle B. Phelps, of Columbia University, and E. S. Keeping, of the University of Alberta, for lending their mathematical brains to some of the problems raised by the returns; to Professor F. C. Koch, of the University of Chicago, for kindly supplying the urine extract administered to one group of crows; to Professor J. B. Collip for the placental extract used on another group; to Professor George Hunter, of the University of Alberta, for the pituitary extract also used; to Mr. W. E. Rose, of Edmonton, for help in trapping; to his technician, Mr. Robert Lister, for his constant assistance in the field as well as in the laboratory; and lastly, to Mr. J. Thompson for his efficient care of the crows during the experiments. To the numerous people in Alberta, in other Provinces and in the Northern United States, to whose interest and coöperation we owe the very gratifying percentage of returns that we are able to show, the writer is particularly grateful.

During the last few years the effect of light on the reproductive systems and activities of birds and mammals has received a great deal of attention

in laboratories on both sides of the Atlantic. To adequately discuss the biological implications of the present undertaking, a summary of such related work is essential. To avoid an unduly lengthy paper it is proposed to divide the account into two sections. The first, herewith, describes the methods employed and the final distribution of the liberated crows. An account of the histology of the collected material, a summary of relevant work carried on elsewhere and a full discussion of the theoretical aspects of the case will be presented in the second.

Trapping took place at Beaverhills Lake, Alberta, on the land of Mr. Arthur Francis who gave us every facility at his disposal, during August, crows of all ages and both sexes being indiscriminately taken. A few young could still be identified by their plumage but the number was so small as to be of no practical value. An attempt had been made earlier in the summer to induce schoolboys throughout the Province to rear young crows and then to sell them to us, but only two birds were thus acquired. A group composed entirely of birds of the year that had never previously migrated would have proved an interesting adjunct to the undertaking.

The crows were shipped to Edmonton in batches of 50 as obtained and there turned into 2 large flying cages till treatment commenced on the 15th of October. In all, nearly 500 birds were captured. We had a number of escapes in the field and at first a high rate of mortality in Edmonton. After periodical samples had been taken during the course of the experiments, 264 crows were finally liberated on November 26. Although the numbers of some of the groups were small, the behavior of the birds, as will appear below, was in most cases consistent.

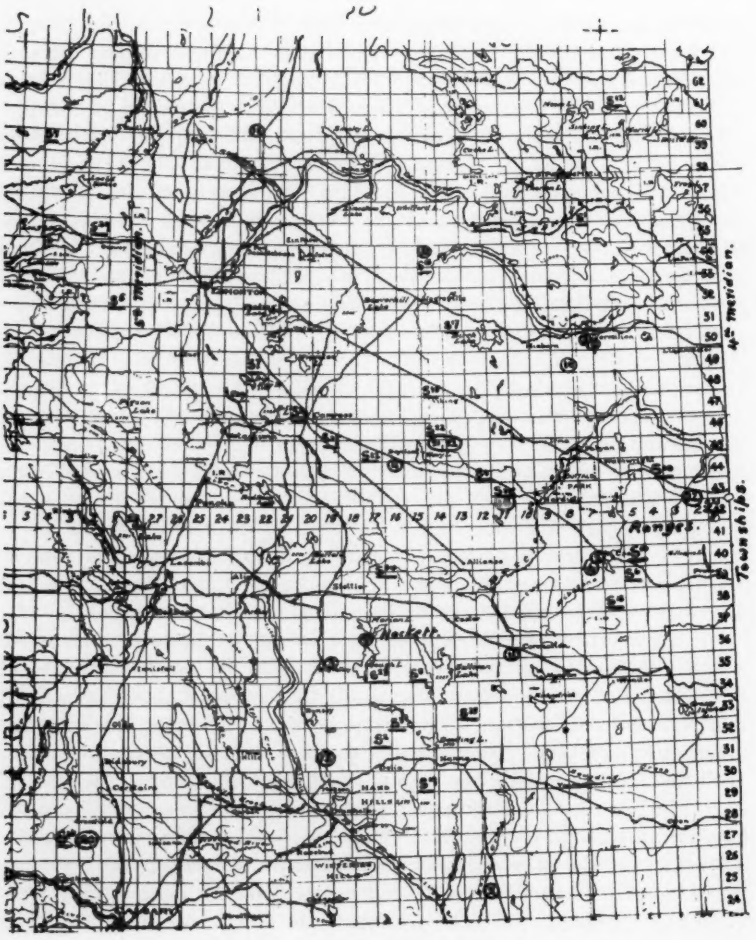
As explained in a previous publication,[3] Edmonton was not a suitable center for the liberation of the birds on account of the large tracts of unsettled or partially settled territory to the northwest, the direction in which the experimental birds might be expected to go. It was therefore decided to transport them by plane to some point in the southeast of the Province where they would have most of inhabited Alberta to the northwest of them. Medicine Hat (330 miles southeast of Edmonton), not only suitably situated, but also an airport, was selected. The time provisionally chosen for departure was 6 A. M. on November 24, the various extracts employed being timed so as to finish up on the 25th, giving us one day's grace in case of unfavorable weather.

The 24th dawned with a pall of fog stretching from Alaska to Winnipeg which held till 10 A. M. on the 26th, when word came through from the airport to say that a start could be made. Assembling all available help immediately, the crows were caught, checked, crated and loaded into the plane at the airport by 1 o'clock, when we took off and headed for Medicine Hat. Both on account of the injected birds and the possible return of fog it was deemed inadvisable to postpone the start any longer, but the late

hour was regrettable. By 3 o'clock, when it was quite certain that we could never make Medicine Hat before dark (there was no night equipment on the plane) and a descent there and then would just give us time to return to the Edmonton port by dusk, we decided to land near the next railway station so as to give us a definite point on the map. This proved to be the village of Hackett, 110 miles by air from Edmonton (see maps). As far as we could observe from the plane at 4000 feet the surrounding country was all farmed. The temperature was about 10° F., the barometer high (27.95), but falling slowly, weather fine with a strong southeast wind and the ground snow-covered. On account of the lateness of the hour all the crows were liberated here together. It was originally planned to make three descents ten miles apart (east and west) and to turn the birds out in three separate batches to avoid interference of one group with another.

Returns have been very satisfactory with 58% of the birds recovered. The large north-bound group, with the lowest figure of 48% recovered, has materially lowered the average. The returns for all other groups were much higher (for details see below), in one case 100% being retaken. Radios and newspapers coöperated generously in Alberta and Saskatchewan, as well as in Montana and the Dakotas, where Professors Allan Mail, of Bozeman, and O. A. Stevens, of Fargo, were primarily instrumental in organizing an efficient watch. This was particularly desirable since, in the event of the north-bound group again contributing poor returns (as in 1929), negative results from the south, if adequately patrolled, would have some significance. And 1929 did repeat itself in this regard.

To increase the chances of returns from this group, still the one of primary interest, the 155 birds involved were conspicuously marked with a band of bright yellow *Duco* across the tail, both above and below. This was sprayed on by an auto-finishing expert. We found this the most satisfactory solution of the marking problem. It interfered in no way with flight or other activities and has evidently proved quite permanent as one or two of these birds have subsequenty returned to Alberta to breed with their tails still bright yellow, more than six months after the application of the paint. It was hoped that by so marking the birds the curiosity of observers would be sufficiently aroused, even if they were completely ignorant of the experiments, to shoot such individuals on sight, when the U. S. Biological Survey band on the leg would ensure the information ultimately reaching us. Every crow was banded. (The capons, for easy recognition while in our aviaries, carried two bands, one on each leg.) The yellow tails also served to distinguish birds of this group from wild crows and from the other groups and added a value to sight records that was entirely wanting in the 1929 experiments. From this viewpoint they served their purpose well, although, bright as they were, under certain lighting conditions the yellow was not visible.



MAP 1

Distribution of wild crows during the winter 1931–2. Figures in circles represent localities from which single crows were received in the flesh: S^c indicates a sight record, or place where an unbanded crow was shot but not submitted to us. Only three wintering flocks were recorded: (1) in the Peace River country, 150 miles off the map, NW; (2) north of Vegreville (T52:R14:W4); (3) south of Viking (T47:R14:W4). For full description, see text.

Food for all groups consisted of unlimited poultry laying mash, hog's liver, the entire output of dogs and cats from the city pound, several horses, rotten eggs *ad lib.*, whitefish which happened to be available in hundreds of pounds, bread (about 50 stale loaves per week) soaked in butter-milk, cracklings, and cabbage and lettuce and other greenstuff.

Returns and Descriptions of Maps.—MAP 1.—Before considering the returns of the captive groups, comment on the wild birds obtained in the Province-wide hunt for crows is apposite. In our preliminary radio and newspaper campaign it was made perfectly clear that *any* crows, unbanded as well as banded, were wanted by us. The request was made for two reasons. Examination of such wild birds as had failed to migrate was a matter of particular interest, with direct bearing on the theory on which the experiments are based. This aspect, in light of the ample material available, will be fully dealt with in the second paper. Secondly, it might conceivably throw light on the distribution of observers, since an overwhelming majority of such wild birds are singletons and more or less evenly scattered through central Alberta which is all good crow country during the summer. Twenty-five wild crows were received in the flesh, the majority in sufficiently good condition for full examination. Their distribution is shown on Map 1, figures in circles indicating localities and the order in which such birds were received. S^s indicates sight records of black-tailed crows, presumably wild birds, although the ones lying southeast of Hackett may include some of our controls. The complete absence of records from the west, northwest and southwest of Hackett will immediately be apparent: the area is relatively poor and sparsely settled.

Several records lie outside the area of the map, including a single bird from Edson in the foothills of the Rockies, 120 miles west of Edmonton; single birds from Wanham and Clairmont, 240 and 200 miles northwest of Edmonton in the Peace River country; and two birds from a large flock at Grande Prairie, also in the Peace River block.

Only three flocks of crows that remained in Alberta for the winter were located (north of Vegreville; south of Viking; at Grande Prairie) and, after considerable effort, samples were ultimately obtained from each.

Numerous records from both Saskatchewan and Manitoba indicate a similar general distribution of single crows, with rarely enough birds together to constitute a flock. Single wild birds were also killed in Montana and North Dakota. Records from South Dakota appear to have been somewhat more frequent, while correspondents from Nebraska consider the crow a more or less regular winter resident.

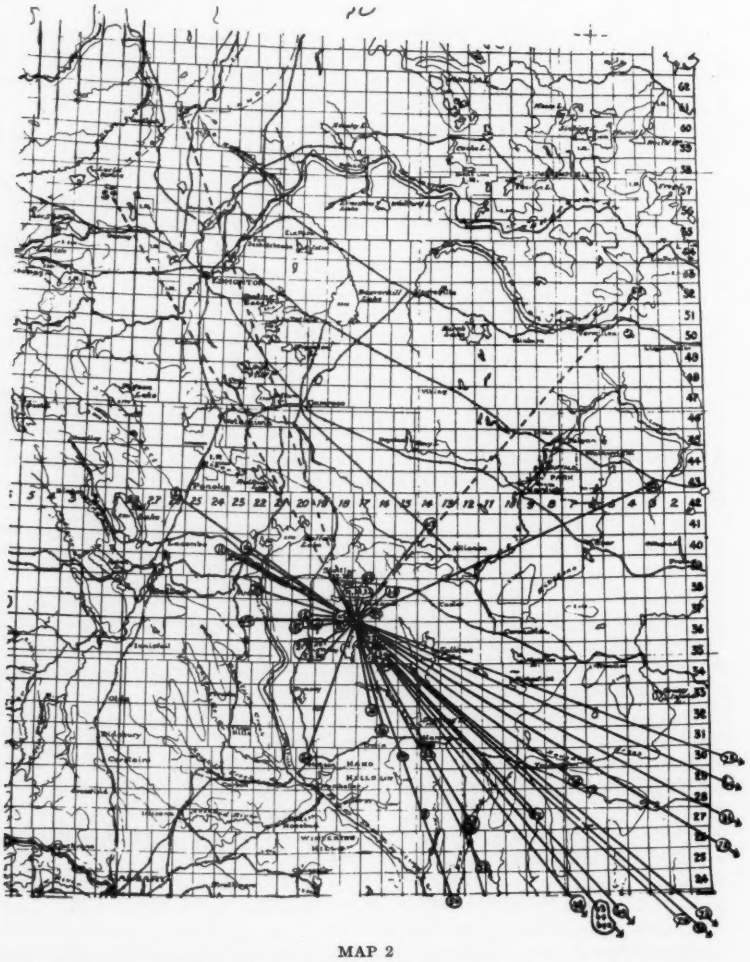
The crow records from the annual Christmas census organized by and published in "Bird Lore"[4] have been mapped. From Iowa eastward the American crow population evidently reaches its maximum winter density, thinning out again south of Kentucky and Virginia and it is probably in the western section of this area that the summer hordes of crows from Alberta pass the winter. Practically all our southbound birds were returned from along a fly-line in this direction, the distance record coming from Wilsonville, Nebraska, virtually on the Kansas boundary line.

MAP 2.—Group A^1. *Experimentals* (Yellow tails). 155 birds liberated Nov. 26 at Hackett, Alberta. 75 birds recovered (up to March 31, 1932) = 48%. 50% of the recoveries may be considered sedentary, although the lateness of many of the recoveries from Hackett does not preclude the possibility of a trip north and subsequent return south.

These birds received lighting in the evenings exactly as previously described,[3] the nightly increase being $7^1/_2$ minutes and the source of illumination ordinary electric light bulbs. The lights were turned on daily at sunset, illumination commencing on October 15. After November 17, when the lights for the first time burned till 11 P. M., the period

was not further extended. It remained at 11 P. M., till the night of the 25th, the day before liberation.

The birds kept fit and active during the lighting period, showing an appreciable average increase in weight at the end. At times of low temperatures (20° to 30° below zero F.) they tended to become somewhat lethargic and inclined to remain in their shed.



MAP 2

Distribution of experimentals (group A^1: yellow tails). The dotted lines (S^2) indicate sight records; numbers in circles, birds shot or trapped (as nearly as possible in chronological order). The numbers of 18 birds recovered at Hackett have been omitted. For full account, see text. *Direction of flight, weighted mean*—NW quadrant, 32° N. of W. In SE quadrant, 38° S. of E.

Four sight records are included on the map (dotted lines, S^s). They indicate yellow-tailed birds seen at close range but not procured. S^1 and S^2 were undoubtedly the same bird seen within a few hours on two farms (feeding with the chickens) four miles apart on December 12. S^3 was a single crow seen on December 10. S^4 includes three birds together, all yellow-tailed, seen on December 12, 145 miles northwest of Hackett.

The numbers of eighteen birds actually retaken at Hackett have been omitted from the map, due to the exigencies of space.

The most interesting recoveries on this map are those from the northwest quadrant. Comparison with Map 1 reveals the fact that these birds again, as in 1929, were traveling into unsettled territory with a dearth of observers. On this ocassion it was due to the unfortunate circumstances that prevented the completion of the journey by air and forced a premature descent at Hackett. Of the records in this direction, L was a single bird taken on December 22, 65 miles northwest of Hackett. It was emaciated and had evidently been detained in a trap as its band and the leg that had carried it were gone (the tail was sent in to us). 11, trapped on December 1, was one of a flock of 6, all yellow-tailed; 16, shot on December 2, was one of a flock of 7, all yellow-tailed; 31 was "one of a flock," all yellow-tailed; 44 was a singleton which arrived about December 1, settled down and was subsequently trapped. Although the numbers actually recovered are thus very small they represent (including the long-distance sight records from this quadrant) some 30 birds. But for the accident of having to liberate them to the east of a sparsely settled region continuing west to the mountains there is little doubt that the returns might have been greatly improved. (Eight more records fall into this quadrant but they are all less than 12 miles from Hackett.)

Thirty birds have been recovered from the southeast quadrant but there are in addition many sight records of yellow-tailed birds. The long-distance record is held by a crow shot in February at Wolsey, S. D. (820 miles). Other birds recovered outside the borders of the Province include 5 from Saskatchewan, 4 from North Dakota and one from Montana. The best time was made by a bird from Washburn, N. D. (600 miles) killed on the 14th of December, 18 days after release, giving an average rate of 33 miles per day. This probably represents good going for a crow. The rate was, however, exceptional. All others that left our boundaries (even the Saskatchewan birds) were killed in 1932.

Big Valley (12 miles from Hackett), in the southwest quadrant, appears to have exerted a strong influence on our birds as it attracted some from all groups. Whatever the explanation, crows from this spot may be disregarded since all groups are affected. The distance is short enough to be accounted for by mere wandering. A single bird, 69, shot at Munson on January 16 thus becomes conspicuous as the solitary crow from this quadrant. In the opposite direction (NE) there is a single sight record, already referred to, and two birds collected on the 20th (No. 47) and the 26th (No. 51) of December at distances of 40 and 96 miles, respectively. These birds will be alluded to again below.

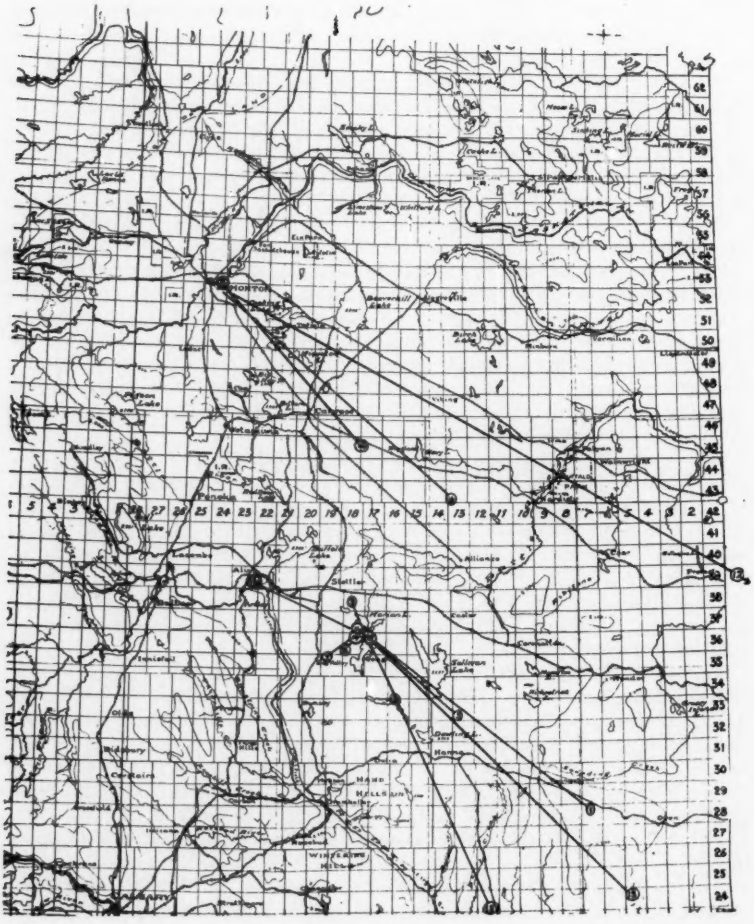
MAP 3.—Group A^3. *Experimental Capons* (Black tails). 24 birds liberated, 19 at Hackett, Nov. 26; 5 at Edmonton, Nov. 27. 17 birds recovered (up to March 31, 1932) = 71%; 41% of these proved sedentary.

Except that these birds had been castrated (males only) their treatment was exactly that of the preceding group; they were housed in the same aviary. There was a marked increase in weight.

A majority of these birds undoubtedly traveled and traveled relatively fast. No. 1 holds the speed record, having been killed 80 miles from the point of release on the morning of the 29th, i.e., he had covered more than 30 miles per day. The distance record is held by No. 12, killed at Anglia, Saskatchewan (270 miles), on about the 15th of

December. All birds took the southeast quadrant with one exception. Nos. 7 and 9 were mere wanderers. No. 9 had achieved exactly 10 miles in 10 days.

No. 16, the only bird of the whole series outside of the Experimentals to go north-

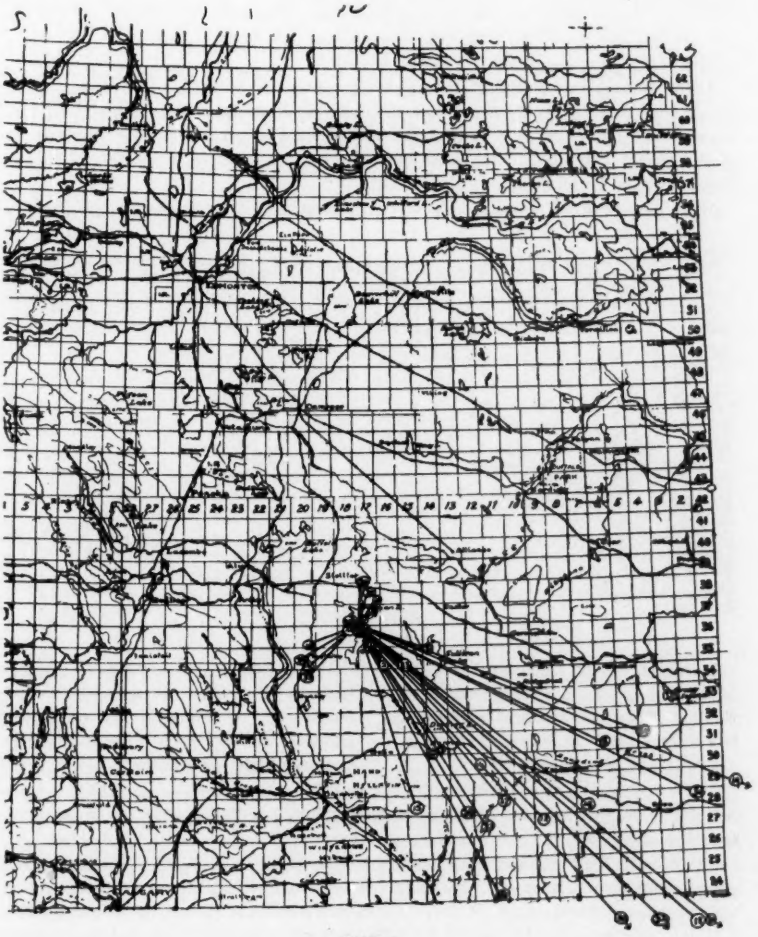


MAP 3

Distribution of experimental seasons (group A^2). Five birds were released at Edmonton; the remainder [illegible]. For full description, see text. *Direction of flight, weighted mean*—Edmonton [illegible], 31½° S. of E. Hackett group, 48½° S. of E.

west, is perhaps the most interesting single bird of the entire undertaking. Unfortunately his body was not received and examination impossible. In castrating our birds, in two cases a single testis was dropped into the body cavity after removal and could

not be recovered. This bird was one of the two. He was taken at Alix (T39:R23:W4) on February 26, 1932. Where he had been in the interim is, of course, unknown and in view of the time that had elapsed after release, chance wandering cannot be



MAP 4

Distribution of controls (group B^1). For full description, see text. *Direction of flight, weighted mean*—$41^1/_4°$ S. of E.

eliminated. If, on the other hand, the testis had accidentally grafted itself, this bird might actually belong to the Experimental (A^1) group.

MAP 4.—Group B^1. *Controls* (Black tails). 53 birds liberated at Hackett, Alberta,

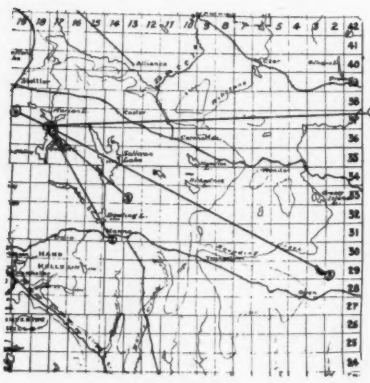
Nov. 26. 34 birds recovered (up to March 31, 1932) = 64%. 38% of these were sedentary.

This group and the remaining B groups, received no artificial light. On October 15 their day ceased at 6:40 P. M. (approximately an hour after sunset) and on Nov. 25 at 5:30 P. M. Sunrise was also more than an hour later. Their last day in captivity was thus approximately two and one-half hours shorter than their first.

There was a slight average increase in weight.

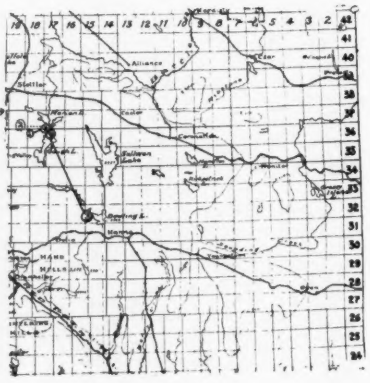
All birds took the southeast quadrant (ignoring the sedentary individuals). The fastest bird was No. 4 which covered 156 miles (to Horsham, Saskatchewan) in three days—over 50 miles per day. This is the speed record for all groups. No. 32 recovered at Wilsonville, Nebraska, 1000 miles from Hackett, in addition, constitutes the long-distance record for all birds.

MAP 5.—Group B^2. *Placental Controls* (Black tails). 9 birds liberated at Hackett,



MAP 5

Distribution of placental controls (group B^2). For full description, see text. *Mean direction* not calculated on account Nof o. 7.



MAP 6

Distribution of pituitary controls (group B^3). The dotted line shows relative site of killing of the single bird liberated at Edmonton. For full description, see text. Sedentary.

Alberta, Nov. 26. 7 recovered (up to March 31, 1932) = 77%. 43% of the recoveries were sedentary.

These birds—the number was limited by the amount of extract available—were normal controls receiving intra-muscular (*pectoralis major*) injections of Professor J. B. Collip's placental extract (A. P. L.), 1 cc. every second day from Nov. 11 to the 23rd. This is a gonadotrophic hormone,* the action of which has been adequately described by Collip[5,6,7] and Wiesner.[8]

The fastest bird, No. 5, had covered 105 miles by Dec. 2 or 18 miles per day. The distance record (from Denzil, Saskatchewan) of 115 miles, is No. 7. This bird is slightly off the correct fly-line, but as he was not killed till Dec. 20 he may have become sedentary after a few days travel and then wandered north. His average speed of less than 5 miles per day is probably indicative of indirect travel.

MAP 6.—Group B^3. *Pituitary Controls* (Black tails). 5 birds liberated; 4 at Hackett,

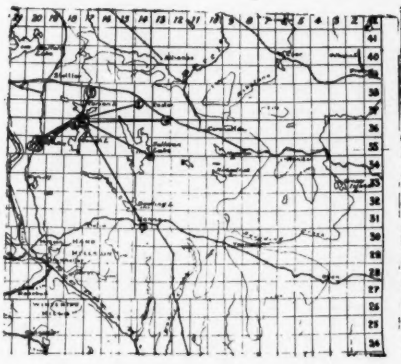
Alberta; 1 at Edmonton, all Nov. 26. 4 recovered = 80%. 75% of these certainly sedentary; possibly 100%.

This small group (originally 10) was receiving intra-muscular injections of pituitary extract (1 cc. per day = 2 gr. anterior lobe) prepared by two methods (Collip; Hill and Parkes) in the Department of Biochemistry, University of Alberta, from the 16th of November to the 25th.

The only bird that had traveled any distance (No. 3) traversed the 33 miles at the rate of 2 miles per day (16 days). The group should probably be considered entirely sedentary.

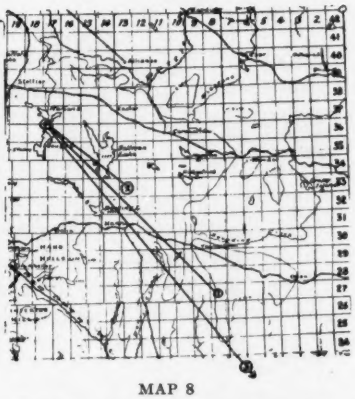
MAP 7.—Group B^4. *Testicular Capons* (Black tails). 15 birds liberated at Hackett, Alberta, Nov. 26. 11 birds recovered = 73%. 100% sedentary.

Castrated (males only) receiving Professor F. C. Koch's extract from human male urine, identical in its action with testis extract. Ten birds received daily intra-muscular injections of 0.5 cc. (5 bird units) of sample U 11 3 from November 11 to 25; the



MAP 7

Distribution of testicular control capons (group B^4). For full description, see text. Sedentary.



MAP 8

Distribution of control capons (group B^5). For full description, see text. *Direction of travel, weighted mean*, 48° S. of E.

remaining 5 received 0.5 cc. (10 bird units) of sample U 11 4 for the same period. Some of these birds showed appreciable gains in weight. See Koch.[9]

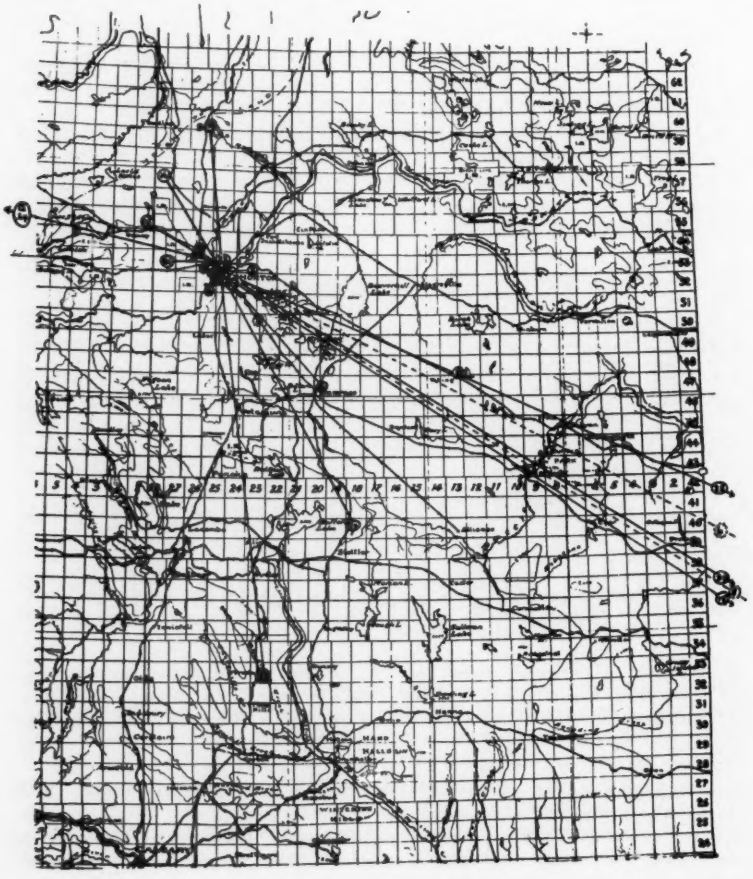
The uniformity in this group, with only 4 birds unheard from, is very striking. The only bird that showed any speed was No. 1, but it covered only 28 miles in three days—9 miles per day. No. 7 which looks so promising as a traveler on the map, took three weeks to get 40 miles. The distribution of the group suggests random scattering.

MAP 8.—Group B^5. *Control Capons* (Black tails). 3 birds liberated at Hackett, Alberta, Nov. 26. 3 birds recovered = 100%. 100% travelers. Castrated birds receiving no treatment whatever.

No. 3 from Maple Creek, Saskatchewan (220 miles) is an interesting bird, since it reached its destination about the middle of December (say 10 miles per day) and took up its residence there through the winter. It was killed (or died) in March when the band was obtained. Both the other crows concerned were killed about the same date and had thus traveled more slowly. Possibly they had both started and later stopped as did No. 3.

MAP 9.—Experimentals and Controls of 1929.

For comparison with the present results, those of 1929 have been herewith mapped. The dotted lines refer to controls and are confined to the southeast quadrant. Except



MAP 9

Distribution of experimentals and controls of 1929 series. The dotted lines indicate controls; the solid, experimentals. *Direction of travel, weighted mean*—in NW quadrant, 28.1° N. of W.; in SE quadrant, 33° S. of E. Weighted average direction of all south-going crows together 39.1° S. of E.

that there are no records whatever from the northeast and southwest quadrants, the similarity between this map and No. 2 (1921 Experimentals) is immediately evident, although the percentage of northwest records is higher for 1929. Details have been already published[3] and need not be repeated here.

Discussion of Maps.—On glancing at all the maps it is evident that all but five significant records are confined either to the northwest or the southeast quadrants. This general direction, as far as we know, is also that of crows migrating to and from Alberta. In this respect our birds are normal. Further, with the exception of some of the two experimental groups (Maps 2 and 9), all birds that have traveled at all have gone southeast (except for the single A^2 bird—see above). These two groups thus come to agree with each other and to differ from all the remainder in that a certain number of birds (aggregating about 35) took the direction of the spring migration—northwest. Reversed migration has thus been successfully induced in at least a percentage of our experimental birds. In no B group whatever has the northwest quadrant been invaded even by a single individual. The low percentage of reversed birds may be due to some misadjustment in our scheme of manipulation or perhaps to some missing factor, but there is no doubt that the southeast fall migration *can* be experimentally reversed. In both years the north-bound birds were heading into sparsely settled territory with very poor chances of recovery. In both cases the percentage of returns was much below that of other groups. In 1931, with their conspicuous yellow tails, these birds should have provided a particularly high rate of recapture had they gone the way of the other groups, yet the opposite was the case. The inference is that a considerably larger number than appears from the records actually traveled northwest.

The effects produced on the birds are undoubtedly transitory. The moment they leave the artificially illuminated aviary they are transferred to a day-length of $5^1/_2$ hours less duration. A point that it has proved impossible to determine is whether, when the effect ceases, the birds become sedentary (a conclusion suggested by the relatively low percentage of returns) or whether they remain active, reverse their direction and return to the southeast. If the latter were the case, and it is quite possible, it would account for the long-distance records from the southeast quadrant. It might also account for the isolated birds in the otherwise untouched quadrants to the northeast and southwest. If bird No. 47 (Map 2) for instance, had gone northwest as far as S^4, remained stationary for a few days and then reversed its direction at a slightly different angle, it might have been killed exactly where it was on the very day that it was (Dec. 20). Both place and date could be so accounted for. On the other hand these odd records may be mere accidents. Even wild birds are known to go astray on migration.

The condition of the gonads in this group was by no means uniform. In some of the males the testes were nearly as large as small doves' eggs; in others they barely showed any signs of enlargement. Generally speaking, recrudescence of the reproductive organs had been induced, but to rather widely varying stages.

Of the controls there is little to say. The high percentage of traveling birds was somewhat unexpected but it proved less surprising than the results obtained from the remaining groups.

The behavior of the capons was wholly unforeseen. The control capons (Map 8), instead of proving sedentary, all traveled southeast. The experimental capons (Map 3), although not quite so uniform, were also southward-bound. These two groups seem to have settled one point. Whatever may be the case with the northward migration, the southward is evidently not associated with the state of the reproductive organs. The movement must depend on some other, at present undetermined, factor.

The other group of capons (Map 7), receiving injections of extracts from male urine, proved to be wholly sedentary. Although no northward tendency was developed, the southern urge appears to have been successfully killed. Again the results are of sufficient uniformity to be convincing.

The placental controls (Map 5) are more doubtful. In the single sample taken before liberation (a female) the ovary showed undoubted development. The only bird returned through the mails was in the same condition. The extract appears to have been effective.

The pituitary controls (Map 6) commit themselves to no verdict at this stage.

Discussion of a possible interpretation of these results is more safely postponed until detailed examination of the material has been completed. That a revision of the original hypothesis is necessary is evident. The facts now, however, are clearer and in many cases conclusive, and an ultimate solution of the problem appears to be very much nearer at hand.

In conclusion, there is one other point that emerges from these returns that is worthy of comment—the faithful adherence of the traveling crows to a specific direction. Both in 1929 and in 1931 a great majority of the birds used were trapped at Beaverhills Lake (T52:R18:W4). All received their treatment at Edmonton, 50 miles further west (where the 1929 birds were also liberated). The 1931 crows were released at Hackett, 100 miles south of the point of trapping, in country that they had in all probability never before seen. Beaverhills Lake on the horizon was visible from the plane at 3000 feet, in perfectly clear weather, till we reached (approximately) township 44. It is extremely doubtful if crows under any circumstances ever attain this altitude. Five hundred feet would probably be very high for a traveling crow. The same general direction is retained by all the south-going groups. The experimental capons (Map 3) illustrate the point particularly well, since some were released in Edmonton and others at Hackett. The mean line adopted by the Edmonton birds is $31\frac{1}{2}°$ south of east; by those from Hackett, $48\frac{1}{2}°$ south of east. If any of these birds were making use of familiar landmarks in the Tofield

country, it is incredible that they should deliberately parallel those landmarks rather than fly over to them and then proceed to follow them. If they are paying no attention to landmarks, but are guiding themselves in some other way, the difficulty disappears. Moreover, some half of the birds were young to whom the surrounding country must have been totally unknown. Winds and sunshine have been suggested by authors as guiding principles for migrating birds. Winds can be ruled out of this case, since there was a strong southeast wind on the 26th and 27th which gradually changed to northwest in the days following. None of the crows traveled in circles to suit the wind. It happened that for a week after the liberations the weather remained fair in southern Alberta and Saskatchewan with only occasional clouds and snowflurries, but that leaves the behavior of many of the experimentals out of the picture. If guiding themselves by the sun, why should they adopt the diametrically opposite direction to the controls?

It is not desired to pursue the topic here, but as experimental evidence of a "sense of direction" in crows, the accompanying facts and maps are extremely striking.

Summary.—Reversal of the southward fall migration has been experimentally induced in crows by subjecting the birds to artificially extended day-lengths for five weeks in October and November. The true percentage of reversals is uncertain but is sufficiently low to indicate that the experimental conditions require adjustment.

Castration does not inhibit the southward passage which appears to be independent of the influence of the gonads.

In the absence of gonads (capons), increasing illumination has no effect, the birds so treated proceeding south like untreated capons. A majority of normal crows that received no treatment whatever also proceeded south.

A wholly sedentary group of caponized crows was, however, produced by means of injections of extract from male human urine. The same is probably true of a group of uncastrated birds receiving injections of anterior pituitary extract. Similar birds receiving placental extract showed a tendency to travel south.

A remarkable "sense of direction" was exhibited by birds that traveled. The migration route characteristic of Alberta crows, from NW to SE and vice versa, was faithfully adhered to by practically all in spite of the fact that they were liberated at what is normally a non-migratory season of the year, in country with which they were presumably unfamiliar, while many of them were young that had never before migrated.

* I am indebted to Professor F. A. E. Crew, of Edinburgh, for the suggestion that use of some gonadotrophic hormone might prove of interest.

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HYDROCEPHALUS, A HEREDITARY CHARACTER IN THE HOUSE MOUSE

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Communicated September 26, 1932

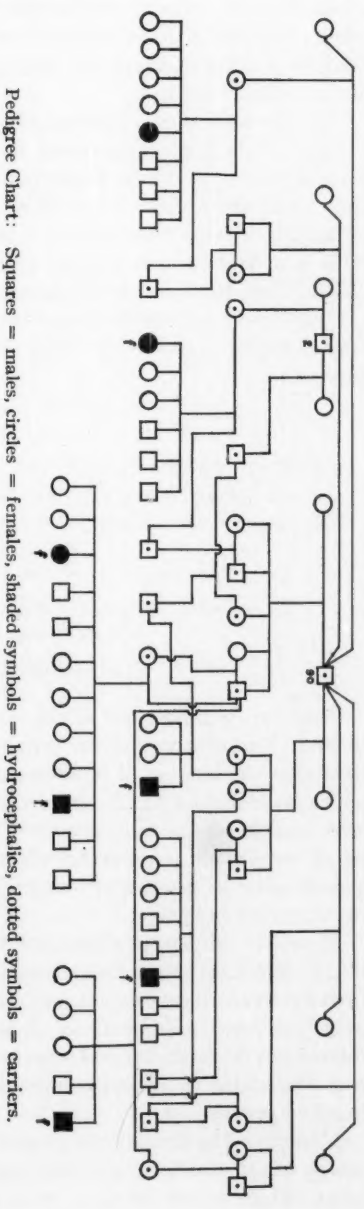
Hydrocephalus has appeared frequently in both the F_2 and back-cross generations of a cross involving flexed tail. Young mice may show a swelling of the head at birth but the character usually does not become noticeable until a week or two later. Hydrocephalic mice become grotesque in appearance, lack coördination in their movements and finally die during the third or fourth week of postnatal life. Superficial examination shows that the bombose skull is caused by the pressure of clear liquid which collects above the brain and distends the roof of the skull outward. The brain itself tends to be pushed downward and forward. When the pressure is relieved by a cranial incision the cerebral hemispheres collapse.

Hydrocephalus first appeared in the back-cross generation of a cross between two flexed tail males obtained from Hunt and several non-flexed females from Little's stock of highly inbred blacks (non-agouti). Neither of these animals nor any of their immediate progeny showed signs of hydrocephalus. When flexed tail individuals of the second generation were backcrossed to F_1 animals, hydrocephalic mice appeared in some of the resulting litters. A classification of the litters in which this character appeared gives a ratio of 35 normal to 7 hydrocephalic. This is a deviation of only 3.5 ± 1.89 from the ratio of 31.5 normals to 10.5 hydrocephalics expected for a mendelizing unit character. These animals and their im-

mediate ancestors are shown in the accompanying pedigree chart prepared through the kindness of Dr. Clyde E. Keeler. Since Hunt has informed the writer that hydrocephalus has appeared in his flexed tail stock, it is apparent that the two P_1 males (nos. 90 and 2) were probably heterozygous for the character. If hydrocephalus is transmitted as a recessive unit character, it follows that half of their offspring would also be hybrid for it and the condition would appear when two such heterozygotes were mated together. The data obtained support this assumption.

Further data indicate that hydrocephalus is transmitted as a simple recessive unit-character as has been suggested above. A flexed tail male extracted from the above-mentioned backcrosses was mated with a naked female. The resulting F_1 animals were mated *inter se* and produced 9 normal and 4 hydrocephalic offspring. One of the F_2 females was backcrossed to her F_1 sire, and although the litter obtained is now but 8 days old, one of the young has a head which is distinctly hydrocephalic. There seems to be little doubt that the P_1 flexed tail male was heterozygous for hydrocephalus and passed the trait on to these two F_1 animals with the result that when they were mated together the character appeared in those individuals homozygous for the hydrocephalus gene.

In the backcrosses shown on the chart, six out of the seven hydrocephalic mice had flexed tails as in-



Pedigree Chart: Squares = males, circles = females, shaded symbols = hydrocephalics, dotted symbols = carriers.

dicated by the letter *f*. While this result could have been due to chance alone, it suggests that the two characters may possibly be linked, or may both be manifestations of the flexed gene since flexed tail occasionally produces normal overlaps.

Since we have shown that hydrocephalus is due to a recessive gene which is lethal in the homozygous form, all of the litters in which hydrocephalics have appeared must have been produced by heterozygous parents. Hence data upon all of these litters may be combined for statistical purposes. When this is done a ratio of 47 normals to 12 hydrocephalics is obtained. This is a deficiency of 2.75 ± 2.24 from the number of hydrocephalics (14.75) expected for a mendelian recessive.

Histological and embryological investigations of this character are under way and will be reported later together with a more complete account of its inheritance.

RATE OF INSTABILITY OF MINIATURE-3 GAMMA GENE OF DROSOPHILA VIRILIS IN THE MALES IN THE HOMOZYGOUS AND IN THE HETEROZYGOUS FEMALES

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Communicated October 14, 1932

From the data obtained in the experiment designed to test the effect of different temperatures on the instability of the gamma-3 gene it was evident that the number of mosaics was approximately the same in females which were diploid for the miniature-3 gamma gene and in males which were haploid for the same gene.[1] The experiments to be described in this paper were made to ascertain the comparative rate of instability of the gamma gene in males and females, both in the homozygous and in the heterozygous condition.

Material.—Miniature-gamma of this experiment came from the same line as that used in the temperature experiment. That line had been inbred for about 70 generations, mostly through mass matings. Miniature-3 beta line had 17 generations of brother-sister inbreedings which were followed by 35 generations of mass matings. The miniature-1 forked stock was propagated by mass matings for seven years, viz., for more than one hundred generations.

Methods.—The miniature-3 gamma gene reverts into its wild-type allelomorph in somatic tissue and the changes, which occur during the development of the wings, produce wild-type regions on the miniature wing.

The frequency of reversions is such that about nine per cent of the flies have mosaic wings and usually not more than one wild-type spot is present on the wing of a mosaic fly.

The number of the wild-type regions in a population indicates the frequency with which the gene changed. In this paper the frequency is expressed in number of mosaic spots found on one hundred flies. By examining the wing under 40.8 × magnification and using weak light reflected from the sub-stage mirror through the wing it has been possible to detect minute wild-type regions and thus to include in the counts practically all mosaic spots.

Miniature is a sex-linked character and therefore females are diploid and the males are haploid for it. To obtain heterozygous miniature-3 gamma females in which mosaic regions could be detected, crosses with constant miniature allelomorphs were made. For this purpose miniature-1 and miniature-3 beta were used.

Results.—Since it has been shown that the temperature does not influence the instability of the miniature-3 gamma gene the data of the temperature experiment[1] are used here again to show the rate of change in the gene in the homozygous females and in the males. These data together with those obtained in new experiments are summarized in table 1.

Discussion.—The results of experiments indicate that in a similar genetic environment each unstable allelomorph changed independently of the other. The rate of the change in homozygous females, having two sets of gamma genes, is 9.54 ± 0.32 per cent and the rate in heterozygous females, having only one set of gamma genes, is 4.51 ± 0.34 per cent.

A similar behavior was observed in case of the unstable rose-alpha gene of the *Delphinium Ajacis*.[2] In heterozygous flowers 1235 changes per one thousand square millimeters were observed and in homozygous flowers the number of changes was 2276.

TABLE 1

SUMMARY OF DATA ON THE FREQUENCY OF MOSAICS FOUND IN THE MALES IN THE HOMOZYGOUS AND IN THE HETEROZYGOUS FEMALES

MATING	NO. OF CULTURES	HETEROZYGOUS FEMALES			HOMOZYGOUS FEMALES			MALES		
		Mosaics	Total	Per cent mosaics	Mosaics	Total	Per cent mosaics	Mosaics	Total	Per cent mosaics
ml-3-γ/ml-3-γ × *ml-1*	6	21	431	4.87	...	...	.....	43	431	9.98
ml-3-γ/ml-3-γ × *ml-3-β*	6	16	413	3.87	...	...	.....	38	413	9.20
ml-3-β/ml-3-β × *ml-3-γ*	10	24	508	4.72	...	...	.....	...	...	.....
ml-3-γ/ml-3-γ × *ml-3-γ*	46	...	...	.....	...	...	.....	...	...	.....
Total	..	61	1352	4.51 ± 0.34	351	3678	9.54 ± 0.32	364	3641	9.99 ± 0.36
					351	3678	9.54 ± 0.32	445	4485	9.92 ± 0.31

In case of the unstable white pericarp of maize, however, Emerson[3] found that the rate of change of heterozygous gene is much higher than the rate of change when the gene is homozygous. This unexpected behavior is, at least partly, accounted for as being due to the effect of modifying factors which are introduced in the material when crosses are made to get the heterozygous females.

The results of experiments reveal a difference in the instability of the miniature-3 gamma gene when located in a male and when located in a female. The rate of change is approximately twice as high in males as it is in females.

It is known that the rate of instability of unstable genes may be readily influenced by several genes.[4] Unstable gene, therefore, is easily affected by its internal environment. Various genes may produce physiological conditions in the cell which make the gene more or less unstable.

It is possible that the difference in the physiological condition of the cell of a male and a female may be responsible for the difference in the instability of the gene in the two sexes. It is, however, equally possible that this difference has nothing to do with the sex but is the result of the female being diploid and the male haploid for the X-chromosome. In case of the unstable reddish, for example, it has been observed that the gene is stable in males and that it becomes unstable in females only when it is in the heterozygous condition. Since triploids are as yet unknown in *Drosophila virilis* it is impossible at present to study the effect of additional chromosomes on the instability of the miniature-3 gamma gene and to obtain in this manner evidence which would make it possible to decide which of the two above-mentioned possibilities is more probable.

That maternal cytoplasm does not affect the instability of the gamma gene is indicated by the fact that the reciprocal crosses gave similar results. The possibility of modifying factors influencing results is also eliminated since crosses with two constant miniatures from unrelated sources gave similar results.

Summary.—Instability of miniature-3 gamma was studied in males and in homozygous and in heterozygous females.

The number of mosaic spots per one hundred individuals was as follows: males 9.92 ± 0.31, heterozygous females 4.51 ± 0.34, homozygous females 9.54 ± 0.32.

The rate of change of the gene, therefore, is twice as high in males as it is in females. In females the rate of instability per gene is the same in homozygous and in heterozygous conditions.

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GLACIAL EPOCHS OF THE SANTA MONICA MOUNTAINS, CALIFORNIA

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Communicated September 28, 1932

Situation and Physiography.— [illegible]r Santa Barbara Islands of southern California are aligned fro[illegible] west to east toward a land-bound member of the same series of upheaved r[illegible]sse[illegible]ch constitutes the Santa Monica Mountains and which, with a leng[illegible] of 45 miles and a width of 10 or 15, reaches inland to Los Angeles, LA, figure 1. These mountains consist, according to Hoots,[1] of deformed Mesozoic and Cenozoic rocks, upfolded in mid-Miocene time. They were then greatly worn down before being broadly upheaved, along with a belt of weak and little deformed upper Miocene beds adjoining on the south, to altitudes of 2000 or 3000 feet in mid-Pleistocene time, in consequence of which they are now deeply dissected, and the belt of weak Miocene beds, much narrowed, is reduced to low relief. The western 30 miles of the southern mountain slope are bordered by the Pacific; there the shoreline is followed below the high-clift ends of the mountain spurs by a fine state highway of recent construction, much traveled as it avoids the heavy grades of roads farther inland.

At the middle of this 30-mile coastal stretch three small ledges of resistant (volcanic?) rock, the eastern one the lowest, the middle one which rises over 200 feet the highest, stand forth in Point Dume, two miles outside of the general shoreline. Back of them a triangular area of the weak Miocene beds, figure 2, measuring 4 miles along its inner, piedmont side, survives the abrasion that has, to the west and east, consumed nearly all that belt and clift the more resistant mountain rocks behind it, some of the cliffs slanting up to a height of 500 or 600 feet. The state highway crosses the triangular area over a 200-foot summit, and its fresh cuts give several clear rock exposures which demonstrate that, before the present epoch, there were two earlier epochs of coastal abrasion, the platforms of which, one now 140 feet, the other, figure 6, 200 feet above sea level, here truncate the gently inclined Miocene beds of the triangle. Occasional boring molluscs, as well as thin veneers of marine cobbles and sands, figure 7, under a cover of subaerial detritus, attest the former presence of the sea.

Three Epochs of Sea Advance.—It thus appears that the Santa Monica coast has suffered three abrasional attacks at different levels by the advancing waves, and the platforms which record these abrasional attacks may be named, in order of height and of time, Malibu (uppermost), after an extensive coastal estate, Dume (middle), after the above-mentioned point, and Monic (present shore), abbreviated from the name of the moun-

tains and of the broadly abraded bay south of them. The Malibu and the Dume platforms are so well shown in the Point Dume triangle that, in spite of the small lengths of the exposures there and in spite of the advanced consumption of the earlier platforms elsewhere by the abrasional retrogradation of the later one, even a hasty observer must recognize their original extension all along the coast. Only one other exposure of the Malibu platform has been found in a western segment of the coast between Sycamore and Sequis creeks, figure 1; and only very short and far-separated exposures of the Dume platform are found to the east and west of Point Dume.

The manifest reason for the better preservation of the earlier platforms

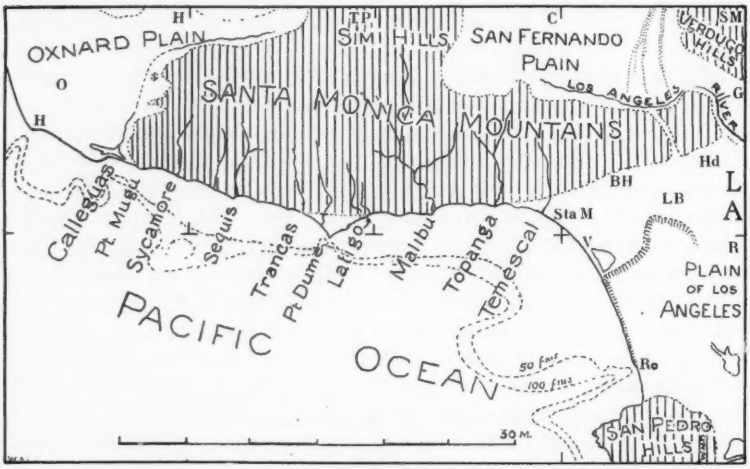

FIGURE 1

Outline map of the Santa Monica Mountains, California.

in the Point Dume triangle is that the Monic cliffs are there held off by all three of the outstanding ledges from consuming the Dume platform above and back of them, as in figure 2; while the Dume cliffs, escaping detention of the low eastern ledge, and receding 800 feet in cobark* outline back of the high middle ledge, but detained on the western ledge, leave a considerable area of the Malibu platform back of and above them, shaded with broken lines in figure 2. Back of this area the Malibu cliffs, greatly subdued since their abandonment by the sea waves, reached an advanced cobark stage a long mile behind the middle ledge, so that their now rounded hills of Miocene beds survive only in a quarter of the present triangular area.

* Cobark is a new term, made up of the initials of its equivalent phrase, cut-out-behind-a-rock-knob, after the fashion of cabal and Anzac.

Two Glacial Epochs of Sea Withdrawal.—Two epochs of sea withdrawal and platform emergence must have alternated with the three epochs of sea advance and platform abrasion; and with the two epochs of withdrawal were associated small uplifts of the mountain mass. Furthermore, during the epochs of sea withdrawal, when the abraded platforms overstrewn with thin, wedge-like deposits of marine detritus were laid bare as infantile coastal plains, the plains were overspread (where they were not trenched by the larger extended streams) with subaerial detritus outwashed by the smaller streams and down-crept from the spur-end cliffs and from the mountain slopes above them. These deposits, which fill the dihedral or shoreline angle between cliffs and platform, constitute the Budu and the Memo covers of the platforms, their names being formed from the adjoining syllables of the three, abrasional-epoch names. When the covers are cut back and clift their remnants, behind which the rock cliffs are concealed, will be called cover-heads.

Along the western 10 miles of the coast the Dume shoreline stands 25 or

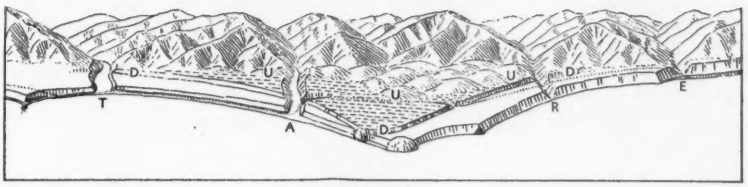

FIGURE 2

Simplified diagram of the Point Dume triangle. *U,U,U,* weathered cliffs of Malibu shoreline; *D,D,D,* cliffs of Dume shoreline. *T,A,R,E,* Trancas, Zuma, Ramera and Escondido creeks.

30 feet above present sea level. The Memo lowering and withdrawal of the sea from that shoreline and the Monic rise and advance of the sea to the present shoreline are best explained, following Daly,[2] by the waxing and waning of a late Glacial epoch; the change of level may have been 250 or 300 feet. The failure of the sea to return now to its former or Dume level is apparently due to the lower temperature of the present Postglacial epoch, in which ice-sheets linger on Greenland and in Antarctica, as compared to that of an earlier and warmer, Interglacial epoch. To be sure, the Memo withdrawal and the Monic return of the sea might be ascribed to an uplift and a depression of the land; but that would in the first place require a depression about equal to the previous uplift, which is inherently improbable, and would in the second place leave out of account the unquestionable changes of sea level due to Glacial variations of climate, the equable nature of such changes of level being their most essential characteristic. But the gradual rise of the Dume shoreline from a 25- or 30-foot

altitude in the western 10 miles of the coast to 140 feet at Point Dume and to 250 feet or more in the easternmost coast must manifestly be explained by an eastward-increasing uplift of the mountain mass. This uplift presumably took place in Memo time, before the return of the abrading Monic sea.

The Budu withdrawal and the Dume return of the sea are likewise best explained by the waxing and waning of an earlier Glacial epoch. The uplift of the coast therewith associated appears to have increased from a small measure at Point Dume to about 170 feet farther west.

The Gratifying Features of Confirmation Bight.—A strongly clift, interheadland bight, figure 3, in the Sycamore-Sequis coastal segment, figure 1, confirms the sequence of events inferred from the road-cuts in the Point Dume triangle in the most gratifying manner, and also affords some additional information. In the first place, the survival here of the Budu and

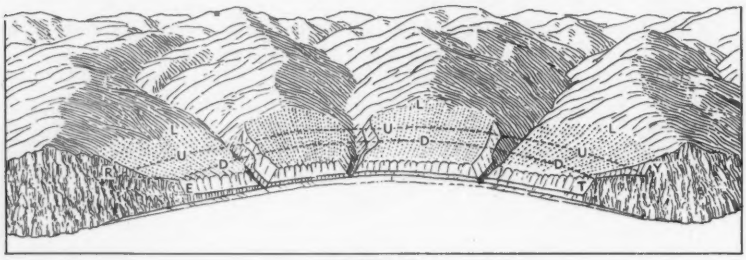

FIGURE 3

Idealized diagram of Confirmation Bight. *E,T,* entrance and exit sections of Dume cliffs; *R,Y,* entrance and exit sections of Malibu cliffs. *D,D,D,* top of Dume cliffs under their Memo cover. *U,U,U,* Malibu shoreline under its Budu cover. *L,L,L,* weathered Malibu cliffs over head of Budu cover.

Memo cover-heads across the middle half-mile of the bight, while the covers are completely cut away in the Monic cliffs of the bold, bight-limiting headlands, show that the Malibu shoreline was more sinous than the Dume and the Dume more sinous than the Monic. When this was perceived it was seen also that the Malibu and the Dume cliffs and platforms must be concealed behind and beneath the cover-heads, and after persistent search they were duly found. A small high-standing exposure of the Malibu platform occurs in a ravine where steeply inclined, resistant and well truncated, mountain-making strata bear a veneer of cobbles under a cover of subaerial detritus at an altitude of about 160 feet; and as the mountain slope begins a rapid ascent to a much greater altitude a little way farther inland, the Malibu cliff-base shoreline, concealed by its Budu cover, is inferred to have an altitude of somewhat less than 200 feet at the foot of that slope.

Several low-lying exposures of the Dume platform are found along the shore under its heavy and strongly clift Memo cover-head which, blending with the degraded Budu cover above and back of it, must have a thickness of 200 or 300 feet near the concealed Dume cliffs. One beach exposure of the platform, figure 8, shows a striking contrast between vertical, truncated, mountain-making strata and their level-bedded, indurated veneer of marine sands and cobbles. Moreover, inasmuch as the Memo cover-head, occupying the middle half-mile of the bight, must stand between the concealed Dume cliff behind it and the visible Monic cliff, refreshed in the way-side

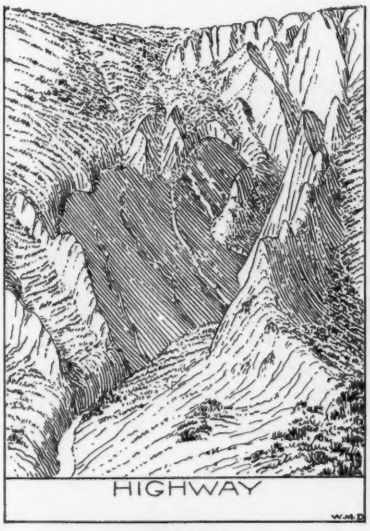

FIGURE 4

The Dume cliff face in a ravine-head of Confirmation Bight.

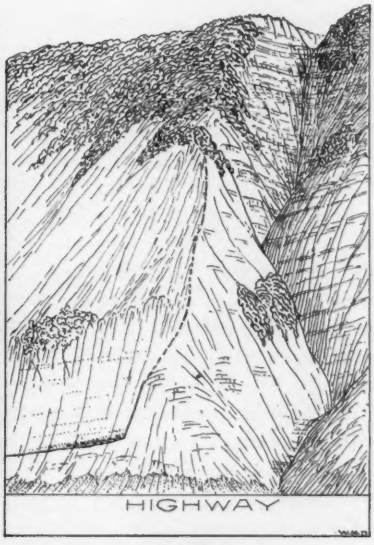

FIGURE 5

Exit section of the Dume cliff with its platform, Confirmation Bight.

cut of its front face, sections of the Dume cliffs should be seen where the clift rocks of the headlands are adjoined by the clift detritus of the cover-head; one, *E*, figure 3, showing the oblique entrance of the cliff into the bight back of the cover-head; the other, *T*, its oblique exit.

Both have been found. The entrance section does not reveal the base of the cliff, because the highway bench, which is there rather high above the beach, conceals it; but the exit section, figure 5, where the highway is a little lower, shows, although obscured by downwashed silt, not only the cliff to a height of perhaps 80 feet, but also the shoreline angle at the cliff base and some 50 feet of the platform with a veneer of marine gravels and

cobbles, the angle between cliff and platform being heavily filled in with Memo detritus. Three additional exposures of the Dume cliff face, one of which is drawn in figure 4, are made where ravines near the entrance and exit sections have removed the Memo cover. I have given this mile of the shore the name, Confirmation Bight, because its highly significant features were found, not by wandering observation before a theoretical analysis of coastal development had been made, but by directed observation after it had been made. Entrance and exit sections of the Malibu cliffs, *R, Y*, figure 3, have been searched for high on the Monic cliffs of the headlands but not found; they are presumably hidden under creeping detritus.

Additional Items.—To the west of Sycamore Creek no records of the Malibu interval and only a few imperfect records of the Dume-Memo interval have been found, because the recession of the Monic cliffs there is so strong as to consume the work of the earlier intervals. No record of the Malibu interval has been found east of the Point Dume triangle, but several good sections of the Dume platform and its Memo cover have there been identified at eastward-increasing altitudes.

Beyond the eastern end of the coast as limited by the Monic cliffs of Santa Monica Bay excavated in the uplifted Dume platform, the Memo platform cover, with a mountain-border thickness of 200 or 300 feet, extends eastward along the base of the mountains for 10 miles or more as a sloping, piedmont, detrital plain, dissected by many ravines. An excellent airplane view of the northwestern part of this area is given in one of Hoots' plates.

At three points along the coast indications are found of a subordinate withdrawal and return of the Monic sea, suggesting a brief Glacial episode rather late in the Monic interval. No space for their description can be given here.

Glacial Chronology of the Coast.—Although the Budu and the Memo withdrawals of the sea are confidently believed to mark the on-coming of two Glacial epochs, it must be understood that no record whatever of actual glaciation is to be found on the Santa Monica Mountains; they are far too low for such records, of which the nearest examples, the southernmost in California and the United States, are found at a much greater altitude

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DESCRIPTION OF FIGURES 6, 7 AND 8

Figure 6.—Road-side section of the Malibu platform truncating inclined Miocene beds, with veneer of marine cobbles and sands under Budu cover of subaerial detritus. Height, about 15 feet. Point Dume triangle. Photo by U. S. Grant, 4th.

Figure 7.—Detail of same. Photo by J. H. Maxson.

Figure 8.—Detail of Dume platform on beach of Confirmation Bight; vertical strata truncated and covered by an indurated veneer of marine cobbles and sands. Photo by U. S. Grant, 4th.

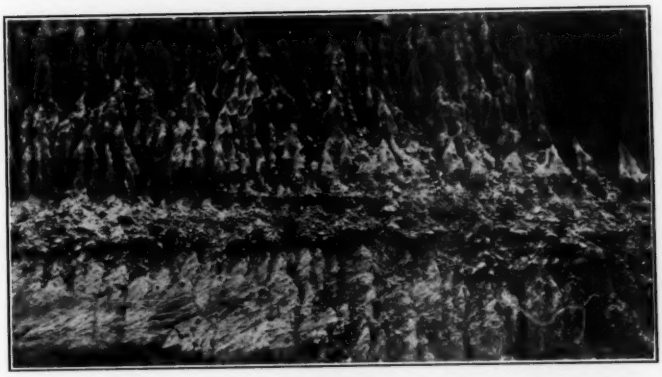

FIGURE 6

FIGURE 7

FIGURE 8

(For description of figures see opposite page.)

in the San Gabriel and the San Gorgonio mountains about 40 and 90 miles to the east. But when it comes to matching the Glacial epochs of the coast with those of the Sierra Nevada as lately studied by Blackwelder,[3] or of the northeastern United States, difficulty is encountered. A simple solution of the difficulty would be to equate the Budu coastal epoch with the next-to-last Glacial epoch, the Tahoe stage of the Sierra Nevada; and the Memo coastal epoch with the last Glacial epoch, the Tioga stage of the Sierra; but that stage seems too brief for the accumulation of the heavy Memo cover, and too recent to be followed by the great abrasional excavation of Santa Monica Bay by the advancing Monic waves. If escape from this embarrassment is sought by shifting the Budu and the Memo intervals back to the Sherwin and Tahoe stages of the Sierra Nevada, then the coastal record of the late Monic episode of sea withdrawal and return seems too brief to correspond even to the short-lived Tioga stage. The glacial chronology of the coast is therefore left uncertain for the present.

[A fuller discussion of the problem here outlined will shortly appear in the Bulletin of the Geological Society of America.]

[1] W. H. Hoots, "Geology of the Santa Monica Mountains, California," *U. S. Geol. Surv.*, Prof. Paper 165 C (1930).

[2] R. A. Daly, "Swinging Sea Level of the Ice Age," *Bull. Geol. Soc. Amer.*, **40**, 721–734 (1929).

[3] Eliot Blackwelder, "Pleistocene Glaciation of the Sierra Nevada," *Bull. Geol. Soc. Amer.*, **40**, 865–922 (1931).

THE COMMUTATOR SUBGROUP OF A GROUP GENERATED BY TWO OPERATORS

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Communicated October 3, 1932

Suppose that the group G is generated by the two operators s and t, and consider the commutators formed by powers of s and t. These commutators are of the form $s^{\alpha}t^{\beta}s^{-\alpha}t^{-\beta}$ and if we transform such a commutator by s or by t there obviously results an operator which is the product of two such commutators or of inverses thereof. It therefore results that the group generated by the commutators of the powers of s and t is an invariant subgroup C of G. The group generated by C and s is invariant under t and its quotient group with respect to C is composed of invariant operators under t. Hence C is the commutator subgroup of G. That is, *if a group is generated by two operators its commutator subgroup is generated by the commutators of the powers of these operators in order.*

In the special case when these two operators are both of order 2 their commutator is $(st)^2$ and hence the commutator subgroup of G is cyclic and is generated by $(st)^2$. When st is of odd order its powers are the commutator subgroup of G and the commutator quotient group is of order 2. When st is of even order the commutator quotient group of G is the four group. These properties of th dihedral group are therefore included in the theorem noted at the close of the preceding paragraph. When at least one of the operators s,t is of order 2 it transforms into its inverse, each of the commutators arising from the powers of these two operators. If the commutator of two operators of order 2 and 3, respectively, is of order 2 then these two operators generate either the tetrahedral group or the direct product of this group and the group of order 2. In fact, the other commutator arising from powers of these two operators is then also of order 2 since the two non-identity commutators arising from the powers of two operators of order 2 and 3, respectively, must be of the same order, but this order can have an infinite number of different values.

The group of order 24 considered in the preceding paragraph is a special case of an infinite category of groups which we proceed to develop. Suppose that s is any operator of a given group H and that t is an operator of order 2 such that the commutator $s^{-1}tst$ is of order 2 for every value of s. A necessary and sufficient condition that this condition is satisfied is that all the conjugates of t under H are commutative with t, and hence all of these conjugates are commutative with each other in view of the obvious theorem: *If an operator is commutative with all of its conjugates under a group then every operator of this set of conjugates is commutative with every other operator of this set.* Another obvious theorem which we desire to use in this connection is that *a necessary and sufficient condition that a commutator involving an element of order* 2 *is commutative with this element is that its order is* 2. Hence it results that *a necessary and sufficient condition that all the commutators which involve a fixed element t of order* 2 *while the other element is replaced successively by all the elements of a group H are of order* 2 *is that all the conjugates of t under H are commutative with each other.*

From these theorems it results that if under the given conditions all the commutators of the form $s^{-1}tst$ are of order 2 then the order of the group generated by t and its conjugates under H cannot exceed 2^h, h being the order of H. The fact that this maximal order can be attained results directly from the following construction: Assume that H is a simple isomorphism between two regular groups and that t is the transposition composed of the first letter of each of these regular groups. The group generated by H and t is then of order $h \cdot 2^h$, and the order of its commutator subgroup is 2^{h-1}. This subgroup is composed of the positive permutations in the group of order 2^h generated by the conjugates of t under H. As this group is completely determined by the given conditions it results

that *there is one and only one group of order* $h \cdot 2^h$ *which is generated by an operator of order 2 and a given group of order h such that the order of each of the h commutators which involve this fixed operator and an element of this group divides* 2. The given group of order 24 results when $h = 3$, and when $h = 2G$ is the octic group.

It is known that every symmetric group, except those of degrees 5, 6 and 8, is generated by two of its operators of orders 2 and 3, respectively.[1] As the powers of these operators in order give rise to two commutators of the same order these two commutators must generate the corresponding alternating group whenever the symmetric group is generated by two operators of orders 2 and 3, respectively. If both s and t are of order 3 the four commutators

$$s^2t^2st \qquad s^2tst^2 \qquad sts^2t^2 \qquad st^2s^2t$$

are of the same order. In fact, the fourth is the inverse of the transform of the first with respect to s^2 and the third is the inverse of the transform of the second with respect to the same operator. The first is of the same order as the third because ab is of the same order as ba whenever a and b are group operators. We proceed to prove the following theorem. *If the orders of two operators are given then it is always possible to select these operators so that some of the non-identity commutators arising from their powers are of different orders except in the following three cases: When both are of order* 2, *when one is of order* 2 *and the other is of order* 3 *or when both are of order* 3.

To prove this theorem it may first be noted that if two regular permutations whose common order exceeds 3 differ only with respect to the interchange of two letters then the product of one into the inverse of the other is of order 2 or of order 3 as these interchanged letters are not adjacent or are adjacent in these permutations. From this it results directly that if the order of one of the two given operators is even and the order of the other exceeds 3 then this operator of even order may be represented by a permutation which involves a transposition while the second operator is represented by a cycle which involves the letters of this transposition but no other letter of the permutation representing the first operator. If the letters of this transposition are adjacent in this cycle they are not adjacent in the square thereof and hence the commutators resulting from the different powers of these two operators will have different orders.

Suppose now that both of the operators s and t are of odd order greater than 3 and that the order of t is at least as large as the order of s. We shall assume also without loss of generality that each of the operators s and t is represented by a single cycle and that s is obtained from t by the use of the first letters of t in order with the exception that the last letter of s does not appear in t. Hence the commutator of s and t is of order 2 while the com-

mutator of s and t^2 is of a larger order than 2 as may be seen by considering the cycle in the commutator which involves the first letter of the permutations representing s and t. It remains to consider the case when the order of one of the two operators s and t is 3 while the order of the other exceeds 3. It can be seen by the preceding method that the theorem noted above applies also to this case and hence this theorem is established.

When the common order of the four commutators arising from powers of s and t, when both of these operators are of order 3, is 2 it is easy to verify that each of them is commutative with two of the others. Hence each of them is non-commutative with at most one of the others. These operators therefore appear in pairs of non-commutative operators if they are not all commutative and each of the operators of the dihedral group generated by one of these pairs is commutative with every operator of the dihedral group generated by the other pair. As the product of these two dihedral groups which cannot have more than two common operators is the commutator subgroup of G it is invariant under G and hence there results the following theorem: *If two operators of order* 3 *have a commutator of order* 2 *they must generate a soluble group and the commutator subgroup is the abelian group of order* 2^m *and of type* (1,1,1...).

A very simple special case presents itself when two operators of order 3 have a commutator of order 2 and also a product of order 3. In this case the two commutators s^2tst^2 and st^2s^2t are obviously equal to each other and the three commutators

$$s^2t^2st \qquad s^2tst^2 \qquad sts^2t^2$$

together with the identity constitute the four group. This must therefore be the commutator subgroup of G. By adjoining s to this four group we obtain the tetrahedral group. If it includes t it is identical with G. If it does not include t we may adjoin to this tetrahedral group the invariant operator $(st^2)^2$ and thus obtain the direct product of the tetrahedral group and the group of order 3. Hence there results the theorem: *If the product of two operators of order* 3, *whose commutator is of order* 2, *is of order* 3 *they generate either the tetrahedral group or the direct product of this group and the group of order* 3.

[1] G. A. Miller, *Bull. Am. Math. Soc.*, **7**, 426 (1901).

ON THE DISTRIBUTIONS OF THE ZEROS OF CERTAIN ANALYTIC FUNCTIONS

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Communicated October 8, 1932

In this note there are given some results of a study of the distribution of the zeros of a function of the form

$$f(z) = \sum_{j=0}^{J} \exp\,(\lambda_{jN} z^N + \ldots + \lambda_{j_1} z + \lambda_{j0}), \qquad (1)$$

where J and N are positive integers, and the λ's are real or complex constants. It is assumed that we do not have $\lambda_{0N} = \lambda_{1N} = \ldots = \lambda_{JN}$, and that we do not have $\lambda_{0n} = \lambda_{1n} = \ldots = \lambda_{Jn} \neq 0$ for any $n < N$. It is also assumed that no two terms in the right-hand member of (1) are identical or differ only by a constant factor.

The work reported here is essentially a generalization, in one direction, of certain well-known work by Wilder, Tamarkin, Pólya, Schwengler and others.[1,2,3,4,5,6]

We first arrange $f(z)$ in a certain normal form. The function can be written

$$f(z) = \sum_{m=0}^{M} f_m(z) \exp\,[g_m(z) + \mu_m z^N],$$

where: M is a positive integer; $\mu_0 \ldots \mu_M$, are distinct constants; $g_m(z)$ is an integral rational function of degree less than N; and $f_m(z)$ is either the constant 1 or a function such as $f(z)$ in which N is replaced by a positive integer $N_m < N$. If $f_m(z)$ is not constant, we can write

$$f_m(z) = \sum_{n=0}^{M_m} f_{mn}(z) \exp\,[g_{mn}(z) + \mu_{mn} z^{N_m}],$$

with stipulations similar to the above. And so on. We continue this process of arranging $f(z)$ until it automatically terminates after a finite number of steps.

Let the points $\mu_0 \ldots \mu_M$, be plotted in the complex plane, and let the smallest convex polygon that contains these points in its interior or on its boundary be drawn. We call this polygon the primary critical polygon for $f(z)$, and we denote it by the symbol P. Let the subscripts be assigned so that $\mu_0, \mu_1 \ldots \mu_{M'}$, are the vertices of P in counter-clockwise order, an arbitrarily chosen vertex being denoted by μ_0. Let the side of P that follows the typical vertex μ_α in counter-clockwise order be denoted by L_α. From any point on L_α draw the normal exterior to P. Let $\varphi_\alpha (0 \leqq \varphi_\alpha$

$< 2\pi$) be the angle between the positive real axis and this outward drawn normal. Let the vertex denoted by μ_0 be selected so that $\varphi_0 < \varphi_1 < \ldots < \varphi_{M'}$. From the origin draw the $(M' + 1)N$ rays $R_\alpha^{(\beta)}$ having the equations

$$R_\alpha^{(\beta)} : \text{amp } z = -\frac{\varphi_\alpha}{N} - \frac{2\beta\pi}{N}, \ (\alpha = 0 \ \ldots \ M'), \ (\beta = 0 \ \ldots \ N - 1).$$

We call these rays the primary critical rays for $f(z)$. These rays divide the plane into $(M' + 1)N$ sectors, each of which is bounded by two of the rays and has none of the rays in its interior. We denote the one of these sectors which is bounded on the clockwise side by the ray $R_\alpha^{(\beta)}$ by the symbol $S_\alpha^{(\beta)}$. We consider $S_\alpha^{(\beta)}$ as not including the points on its bounding rays.

Let α be any one of the integers $0 \ \ldots \ M'$. If $f_\alpha(z)$ is not constant, we construct, in the same way, its primary critical polygon, P_α, its primary critical rays

$$R_{\alpha\beta}^{(\gamma)}, \ (\beta = 0 \ \ldots \ M'_\alpha), \ (\gamma = 0 \ \ldots \ N_\alpha - 1),$$

and the associated sectors $S_{\alpha\beta}^{(\gamma)}$. Similarly, if α is one of the integers $0 \ \ldots \ M'$, and if β is one of the integers $0 \ \ldots \ M'_\alpha$, and if $f_{\alpha\beta}(z)$ is not constant, we construct the primary critical polygon for $f_{\alpha\beta}(z)$, the primary critical rays

$$R_{\alpha\beta\gamma}^{(\delta)}, \ (\gamma = 0 \ \ldots \ M'_{\alpha\beta}), \ (\delta = 0 \ \ldots \ N_{\alpha\beta} - 1),$$

and the associated sectors $S_{\alpha\beta\gamma}^{(\delta)}$. And so on. We continue this process of constructing polygons, rays and sectors, until it automatically terminates after a finite number of steps.

We have defined the primary critical rays of $f(z)$; now we proceed to define critical rays "of higher order." A secondary critical ray of $f(z)$ is a primary critical ray of a function $f_\alpha(z)$, $(\alpha = 0 \ \ldots \ M')$, which lies in one of the sectors $S_\alpha^{(0)} \ \ldots \ S_\alpha^{(N-1)}$. A tertiary critical ray of $f(z)$ is a secondary critical ray of a function $f_\alpha(z)$, $(\alpha = 0 \ \ldots \ M')$, which lies in one of the sectors $S_\alpha^{(0)} \ \ldots \ S_\alpha^{(N-1)}$. And so on. Note that in these definitions we have the same value of α in $f_\alpha(z)$ and $S_\alpha^{(\beta)}$.

We are now ready to announce the chief results of the investigation in the form of the following three theorems. The proofs require nothing more than the use of familiar analytical processes, but they are long and complicated. They will be given later in another paper.

THEOREM 1. *There exists a set of half-strips, equal in number to the critical rays of $f(z)$, each extending in the direction of a different one of the critical rays, such that each zero of $f(z)$ is a point of one or more of these half-strips.*

By a half-strip is meant the open set of points between two parallel

straight lines and on one side of a line perpendicular to these. It is natural to classify the half-strips referred to in Theorem 1 as primary, secondary, etc., according to the natures of the critical rays to which they correspond.

THEOREM 2. *The number of zeros of $f(z)$ in a primary half-strip and within the circle $|z| = r$ is equal, for r large, to*

$$\frac{lr^N}{2\pi}\,[1 + 0(l/r)],$$

where l is the length of the side of P which corresponds to the half-strip in question.

THEOREM 3. *The number of zeros of $f(z)$ within the circle $|z| = r$ and in a non-primary half-strip corresponding to a critical ray of $f(z)$ that is a critical ray of a function $f_\alpha(z)$, $(\alpha = 0 \ldots M')$, is asymptotically equal, for r large, to the number of zeros of $f_\alpha(z)$ in the same region.*

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[2] Tamarkin, J. D., *Math. Zeitsch.*, **27**, 1–54 (1927).

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ON THE BEHAVIOR OF THE nth ITERATE OF A FREDHOLM KERNEL AS n BECOMES INFINITE

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Recent researches concerning geometrical probabilities which we will call "linked" (French: *en chaîne*) have demonstrated the importance of the study of the asymptotic behavior of the nth iterated kernels which present themselves in this problem.

We shall define iteration by the formula

$$K^{(n+\nu)}(M,P) = \int_V K^{(n)}(M,Q)K^{(\nu)}(Q,P)dQ;$$

the kernels to be studied in this problem are those for which

$$(P) \qquad K(M,P) \geqslant 0$$

$$(T) \qquad \int_V K(M,P)dP = 1.$$

A summary of the results obtained in this case has been published recently in the C. R. Acad. Sci., Paris.

But the same problem can be extended to the most general kernel, whether or not the conditions (P) and (T) are satisfied.

To solve it, it is good to consider first the simpler problem of studying the asymptotic behavior of the solutions of a system of q linear difference equations of the first order with constant coefficients in q unknowns. When this is done, the only tools needed for the solution of the general problem are the classical Fredholm theory and the notion and theory of the principal kernel due to Goursat, Heywood and Lalesco.

For simplicity, we shall consider the case where the iterated kernels are continuous, after a certain rank m, on the domain of integration V, which is assumed bounded.

Calling L_n the bound of $|K^{(n)}(M,P)|$—which bound is known to be finite when $n \geqslant m$—we shall then be able to classify the several possibilities in the following manner.

1. *L_n is not bounded when n increases indefinitely* (a) if at least one of the fundamental constants λ_j of $K(M,P)$ is < 1, in modulus; (b) or if all the λ_j being, in modulus, $\geqslant 1$, at least one of λ_j is $= 1$ in modulus and is a multiple pole of the resolvent of $K(M,P)$.

2. *L_n has a bound independent of n* (for $n \geqslant m$) in all other cases, that is: (c) if all the fundamental constants, λ_j of $K(M,P)$ be > 1 in modulus; (d) or if the λ_j being $\geqslant 1$, in modulus, all those whose moduli is 1, be simple poles of the resolvent.

Case (c) may be characterized, against the three other ones, as the case where $K^{(n)}(M,P)$ converges uniformly to zero.

Case (d) is the most interesting, inasmuch as the application to linked probabilities is a particular instance of case (d). It gives rise to several possibilities which we shall now discuss, without limiting ourselves to the application to probabilities.

Special Study of the Case Where the Iterated Kernels Have a Common Bound.—The sequence of the $K^{(n)}$ do not generally converge in the usual sense. But in the present case, *it always converges uniformly in the Cesaro way.* That is to say, if we put

$$\mathfrak{M}_\nu(M,P,n) = \frac{1}{n}\left[K^{(\nu+1)}(M,P) + \ldots\ldots\ldots + K^{(\nu+n)}(M,P)\right]$$

where ν is any fixed rank $\geqslant m$—so that $\mathfrak{M}_\nu(M,P,n)$ be certainly finite and even continuous—then, this arithmetic mean converges uniformly in the usual sense to a continuous limit $\Pi(M,P)$, this limit being independent of ν.

The difference $[\mathfrak{M}_\nu(M,P,n) - \Pi(M,P)]$ is infinitely small with $\frac{1}{n}$: it is of *an order which is at least* equal *to the order of* $\frac{1}{n}$.

The *generalized limit* $\Pi(M,P)$ *is a function of "finite rank" r*

$$\Pi(M,P) = \sum_{j=1}^{j=r} \Phi_j(M)\,\Psi_j \quad (P)$$

where Φ_j, Ψ_j *are any biorthogonal and normal system of fundamental solutions relative to the fundamental constant* $\lambda_1 = 1$ *of the associated kernels,* $K(M,P)$ *and* $K(P,M)$. (When 1 is not a fundamental constant of $K(M,P)$, $\Pi(M,P)$ is $\equiv 0$.)

Some *particular cases* (of special interest in the application to probabilities) shall now be examined.

(*A*). $\Pi(M,P)$ INDEPENDENT OF M. *In order that the generalized limit* $\Pi(M,P)$, *be independent of* M, *it is necessary and sufficient that the two following conditions be together fulfilled*

I (P) $\qquad \int_V K(M,P)dP = 1$

II *there be a unique common solution* $X(P)$ *of both the equations*

$$X(P) = \int_V X(Q)K(Q,P)dQ; \qquad \int_V X(P)dP = 1.$$

And then $\Pi(M,P)$ reduces to this *unique common solution.*

In our general hypotheses, the Fredholm determinant $D(\lambda)$ may not have a definite significance, since $K(M,P)$ may be unbounded or even infinite for some pair (M,P). But *in the more particular case where* $K(M,P)$ *is continuous,* $D(\lambda)$ recovers a definite value for each λ and the set of *conditions I and II may be replaced* by the set of conditions I and II′. *The unity is a simple root of* $D(\lambda)$.

(*B*). ASYMPTOTIC PERIODICITY IN n OF $K^{(n)}(M,P)$. *If the fundamental constants of* $K(M,P)$ *whose moduli* $= 1$ *are roots of the binomial equation* $\lambda^N - 1 = 0$, *then* $K^{(n)}(M,P)$ is the sum of a periodic function of n, $A(M,P,n)$ with the period N and of a function $B(M,P,n)$, which converges uniformly to zero when n tends to infinity. The converse property is also true. (It may be proved that the kernels verifying the conditions $(P)(T)$ are special instances where the iterated kernels $K^{(n)}$ are asymptotically periodic functions of n.)

(*C*). USUAL CONVERGENCE OF $K^{(n)}$. *More particularly, the necessary and sufficient condition that* $K^{(n)}(M,P)$ *converges uniformly, not only in the Cesaro sense, but in the usual way, is that* $K(M,P)$ have no fundamental constant of modulus 1 except 1 itself. The limit in the usual sense is still, of course, $\Pi(M,P)$ and may be determined directly in the same way as above. In the present case $[K^{(n)}(M,P) - \Pi(M,P)]$ is infinitely small with $\frac{1}{n}$ *and its order is greater than that of* $\left(\frac{1}{\rho_0}\right)^n$, where $1 < \rho_0 < \rho$, ρ being the smallest modulus of the $\lambda_j \neq 1$.

The above results shall be proved and completed in a separate memoir.

ON THE FUNCTION IN QUANTUM MECHANICS WHICH CORRESPONDS TO A GIVEN FUNCTION IN CLASSICAL MECHANICS

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Let $f(p,q)$ denote a function of the canonical variables p,q of classical mechanics. In making the transition to quantum mechanics, the variables p,q are represented by Hermitian operators P,Q which satisfy the commutation rule

$$PQ - QP = \gamma 1 \tag{1}$$

where $\gamma = h/2\pi i$ and 1 indicates the unit operator. From group theoretic considerations, Weyl[1] has obtained the following general rule for carrying a function over from classical to quantum mechanics. *Express $f(p,q)$ as a Fourier integral,*

$$f(p,q) = \int\int e^{i(\sigma p + \tau q)}\, \zeta(\sigma,\tau) d\sigma d\tau \tag{2}$$

(or in any other way as a linear combination of the functions $e^{i(\sigma p+\tau q)}$). Then the function $F(P,Q)$ in quantum mechanics which corresponds to $f(p,q)$ is given by

$$F(P,Q) = \int\int e^{i(\sigma P + \tau Q)}\, \zeta(\sigma,\tau) d\sigma d\tau. \tag{3}$$

It is the purpose of this note to obtain an explicit expression for $F(P,Q)$, and although we confine our statements to the case in which $f(p,q)$ is a polynomial, the results remain formally correct for infinite series.

Any polynomial $G(P,Q)$ may, by means of relation (1), be written in a form in which all of the Q-factors occur on the left in each term. This *form* of the function $G(P,Q)$ will be denoted by $G_Q(P,Q)$. Let $G_Q(p,q)$ indicate the function of the commutative variables p,q obtained from $G_Q(P,Q)$ by replacing P,Q by p,q, respectively. In a similar manner $G_P(P,Q)$ and $G_P(p,q)$ may be defined. For example, if $G(P,Q) = PQP$, we find $G_Q(P,Q) = QP^2 + \gamma P$, $G_P(P,Q) = P^2Q - \gamma P$, $G_Q(p,q) = p^2q + \gamma p$, $G_P(p,q) = p^2q - \gamma p$.

Our principal result may now be stated as follows. *Let $f(p,q)$ be a polynomial in the canonical variables p,q of classical mechanics, and $F(P,Q)$ the corresponding function of the Hermitian operators P,Q in quantum mechanics. Then*

$$F_Q(p,q) = e^{\frac{\gamma}{2}\frac{\partial^2}{\partial p \partial q}} \longrightarrow f(p,q) = f(p,q) + \frac{\gamma}{2}\frac{\partial^2 f(p,q)}{\partial p \partial q} + \left(\frac{\gamma}{2}\right)^2 \frac{1}{2!}\frac{\partial^4 f(p,q)}{\partial p^2 \partial q^2} + \ldots \tag{4}$$

$$\text{and } F_P(p,q) = e^{-\frac{\gamma}{2}\frac{\partial^2}{\partial p \partial q}} \longrightarrow f(p,q) = f(p,q) - \frac{\gamma}{2}\frac{\partial^2 f(p,q)}{\partial p \partial q} + \left(\frac{\gamma}{2}\right)^2 \frac{1}{2!} \times \frac{\partial^4 f(p,q)}{\partial p^2 \partial q^2} - \ldots \quad (5)$$

In order to obtain $F_Q(P,Q)$ from $F_Q(p,q)$ we need only to write $F_Q(p,q)$ with the q-factors on the left in each term and then replace p,q by P,Q, respectively.

It has been shown that[2]

$$e^{P+Q} = e^{\gamma/2}\, e^{Q}\, e^{P},$$

from which it follows that

$$e^{i(\sigma P + \tau Q)} = e^{-\frac{\sigma\tau\gamma}{2}}\, e^{i\tau Q}\, e^{i\sigma P} = e^{\frac{\sigma\tau\gamma}{2}}\, e^{i\sigma P}\, e^{i\tau Q}.$$

Substituting in (3) we find

$$F_Q(P,Q) = \int\int e^{-\frac{\sigma\tau\gamma}{2}}\, e^{i\tau Q}\, e^{i\sigma P}\, \zeta(\sigma,\tau) d\sigma d\tau$$

and thus

$$F_Q(p,q) = \int\int e^{-\frac{\sigma\tau\gamma}{2}}\, e^{i(\sigma p + \tau q)}\, \zeta(\sigma,\tau) d\sigma d\tau$$

$$= \int\int \left[1 - \frac{\sigma\tau\gamma}{2} + \left(\frac{\sigma\tau\gamma}{2}\right)^2 \frac{1}{2!} - \ldots\right] e^{i(\sigma p + \tau q)}\, \zeta(\sigma,\tau) d\sigma d\tau. \quad (6)$$

But from (2) we see that

$$\frac{\partial^{2n} f(p,q)}{\partial p^n \partial q^n} = \int\int (-\sigma\tau)^n\, e^{i(\sigma p + \tau q)}\, \zeta(\sigma,\tau) d\sigma d\tau, \; (n = 1,2 \ldots)$$

and formula (4) is obtained by substituting in (6). In a similar manner the formula (5) may be verified.

Since $e^{\frac{\gamma}{2}\frac{\partial^2}{\partial p \partial q}}$ is a linear operator it is sufficient to consider the case in which $f(p,q)$ is a single term of a polynomial.

Let $f'(p,q) = p^r q^s$, where r and s are arbitrary positive integers. Then from (4) and (5) we have

$$F'_Q(P,Q) = \sum_{k=0} \left(\frac{\gamma}{2}\right)^k k! \binom{r}{k} \binom{s}{k} Q^{s-k} P^{r-k} \quad (7)$$

and

$$F'_P(P,Q) = \sum_{k=0} \left(-\frac{\gamma}{2}\right)^k k! \binom{r}{k} \binom{s}{k} P^{r-k} Q^{s-k}, \quad (8)$$

the sum in each case being extended to the smaller of r and s. It is not difficult to verify directly by means of formula (10) below that $F'_Q(P,Q) = F'_P(P,Q)$, which we know must be true as these are different forms of the same function $F'(P,Q)$.

A more symmetrical form of $F'(P,Q)$ may be obtained by eliminating γ in (7) or (8) by means of relation (1). We shall now show that

$$F'(P,Q) = \frac{1}{2^r}\sum_{l=0}^{r}\binom{r}{l}P^{r-l}\,Q^s\,P^l = \frac{1}{2^s}\sum_{l=0}^{s}\binom{s}{l}Q^{s-l}\,P^r\,Q^l. \qquad (9)$$

By means of the known formula[3]

$$P^nQ^m = \sum_{k=0}\gamma^k\,k!\binom{n}{k}\binom{m}{k}Q^{m-k}\,P^{n-k}, \qquad (10)$$

we find

$$\frac{1}{2^r}\sum_{l=0}^{r}\binom{r}{l}P^{r-l}\,Q^sP^l = \frac{1}{2^r}\sum_{l=0}\sum_{k=0}\binom{r}{l}\gamma^k\,k!\binom{r-l}{k}\binom{s}{k}Q^{s-k}\,P^{r-k}$$

$$= \frac{1}{2^r}\sum_{k=0}\sum_{l=0}\binom{r-k}{l}\gamma^k\,\frac{r!}{(r-k)!}\binom{s}{k}Q^{s-k}\,P^{r-k}$$

$$= \sum_{k=0}\left(\frac{\gamma}{2}\right)^k k!\binom{r}{k}\binom{s}{k}Q^{s-k}\,P^{r-k}.$$

But by (7) this is $F'_Q(P,Q)$. A similar calculation verifies the second part of (9). The Hermitian character of $F'(P,Q)$ is now evident.

It may be of interest to note how $F'(P,Q)$ differs from the formula proposed by Born and Jordan in 1925.[4] They suggested that p^rq^s should go over into

$$\frac{1}{r+1}\sum_{l=0}^{r}P^{r-l}\,Q^s\,P^l.$$

This is seen to differ from $F'(P,Q)$ in case both r and s are greater than unity.

[1] Weyl, *The Theory of Groups and Quantum Mechanics*, E. P. Dutton & Co., N. Y., 275 (1931).

[2] Kermack and McCrea, *Proc. Edinburgh Math. Soc.*, Ser. 2, **2**, 224 (1931); McCoy, *Ibid.*, **3**, 121 (1932).

[3] Born and Jordan, *Zeits. Phys.*, **34**, 873 (1925).

[4] Born and Jordan, loc. cit., 874.